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April 1912

Editor: JOHN M. COULTER

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THE
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APRIL 1912

OBSERVATIONS ON HETEROSTYLOUS PLANTS

NEIL E. STEVENS

(WITH PLATES XXI–XXIII)

The discovery of the "sex determinant" or "accessory chromosome" in the sperms of certain insects is probably the most notable cytological advance of the present decade. Furnishing, as it apparently does, a cytological basis for the predestination of sex at the time of fertilization, it has an important bearing on the whole question of the determination and heredity of sex. The condition found in these insects has been too widely discussed to need description here. It may be briefly summed up, however, as follows: examination has shown that the sperms are of two classes, equal in number, which differ in respect to one or more of the chromosomes which enter into the formation of their nuclei; and the facts clearly demonstrate that fertilization of the eggs by one class produces males, by the other class females. This difference, the significance of which was first suggested by MCCLUNG in 1902, has been shown to occur in nearly a hundred species of insects (WILSON **40**, p. 57).

Its prevalence here has suggested the possibility of a similar condition in all animals having separate sexes. Attempts have also been made to demonstrate such a condition in dioecious plants, but as yet no positive results have been obtained. Miss SYKES published in 1909 (**39**) a brief note on the nuclei of some dioecious plants. She studied *Hydrocharis Morsus-ranae*, *Bryonia dioica*, *Lychnis dioica*, *Mercurialis perennis*, and *Sagittaria montevidensis*,

and states that the nuclei of the male and female plants were in all cases apparently identical, both in the number and in the character of their chromosomes. More complete studies have been made by DARLING (**5**) in *Acer Negundo*, and by STRASBURGER (**38**) in *Melandrium rubrum*, *Cannabis sativa*, *Mercurialis dioica*, and *Bryonia dioica*. Both writers report that in the reduction division of the microspore mother cells they find no evidence of anything which might be considered a "sex determinant." Negative results in these few cases, of course, do not prove that a sex determinant never occurs in plants, for it will be remembered that such a condition has been demonstrated in only a comparatively few animals.

Dimorphic heterostylous plants present, as will be pointed out below, such striking resemblances to dioecious plants that the present study was undertaken in the hope of finding, in the reduction division of the microspore mother cells, some indication of a morphological difference in the chromosomes which go to make up the nuclei of the microspores.

Material of several species was prepared, but only two, *Fagopyrum esculentum* and *Houstonia caerulea*, proved favorable for study. The material used was all collected in the spring and summer of 1910. The buds of *Fagopyrum* were taken from vigorous plants under cultivation; those of *Houstonia* were nearly all from an old, well-established lawn, where many of the clumps had very likely persisted for several years.

The writer wishes to acknowledge his indebtedness to Professor A. W. EVANS, at whose suggestion this study was undertaken, for assistance in all parts of the work, and to Dr. G. E. NICHOLS for generous aid in the collection and preparation of material.

Historical sketch

PERSOON, in 1794, notes that in certain species of *Primula* there are two forms which exist in about equal numbers and differ from each other in the length of their pistils and stamens. This is, according to VON MOHL (p. 326), the first description of the condition now known as heterostyly.

This condition was apparently regarded as a mere variation in form until the time of DARWIN, who discusses several dimorphic

and trimorphic genera in a series of papers read before the Linnean Society during the years 1862–1868. In these early papers DARWIN (**6–10**) calls attention to the fact that the morphological differences in the flowers constitute a device by which cross pollination is favored, and that these differences in form are associated with physiological differences which affect their fertility, so that a flower of either form is more likely to be fully fertilized when pollinated from a flower of the other form ("legitimate pollination") than when pollinated from a flower of the same form ("illegitimate pollination"). He also describes the offspring of illegitimate unions and points out that they differ from normal plants and have what he calls a "hybrid-like" nature.

DARWIN afterward collected these papers and published them in a "connected and corrected form, together with new matter" in *The different forms of flowers in plants of the same species*, which contains also an account of the literature on the subject up to the date of its publication (1877). Only three of the writers whom he mentions, HILDEBRAND, SCOTT, and MÜLLER, treat heterostyly as anything more than a mere difference in form or at most a device to favor cross pollination.

HILDEBRAND, who first used the term "heterostyled," was also the first to investigate the inheritance of heterostyly. In his first paper (**18**) he describes experiments on the illegitimate fertilization of *Linum perenne* and *Primula sinensis*. The illegitimately pollinated flowers of *Linum* were uniformly sterile. In *Primula*, however, all the illegitimately pollinated flowers developed capsules, which contained an average of 18 seeds, about two-fifths the number found in the capsules of legitimately pollinated flowers. HILDEBRAND planted the seeds thus produced, and found that while the seeds of either form legitimately fertilized produce long-styled and short-styled forms in about equal numbers, the seeds from illegitimate unions tend to reproduce the parent form. Seeds from illegitimate unions of long-styled plants, however, tend to transmit the parent form more truly than those of the short-styled. This conclusion was accepted by DARWIN, but the results he later obtained from similar experiments with *Primula sinensis* do not agree very closely with those of HILDEBRAND.

Two later papers by HILDEBRAND (**19, 20**) deal with trimorphous species of *Oxalis*. He found in *Oxalis Valdiviana* (**20,** p. 43) that seeds from any one of the six possible legitimate unions produced all three forms, but that the two parent forms greatly predominated. He also states that long-styled plants of *Oxalis rosea*, growing by themselves, have always produced long-styled plants ("Jahr aus Jahr ein dieselbe Form entsteht").

In 1864, JOHN SCOTT published a paper (**32**) in which he arranges all the known species of *Primula* in four groups: dimorphic, short-styled, long-styled, and non-dimorphic (homostyled), and describes experiments with 7 dimorphic species. He pollinated each of these 7 species both legitimately and illegitimately and counted the seeds obtained by each method. The result was uniformly that legitimate unions produced a markedly greater number of seeds than illegitimate.

FRITZ MÜLLER (**27**), in a brief paper dealing with a trimorphous species of *Pontederia* growing in Brazil, mentions the fact that in *Oxalis Regnelli*, another trimorphous species, the seeds of long-styled plants, legitimately fertilized with pollen from the longest stamens of the mid-styled form, produced plants which belonged exclusively to the two parent forms.

In his *Forms of flowers*, DARWIN includes all that had been done on heterostylous plants up to the time of its publication. He cites 38 genera known to include heterostyled species. These genera are distributed as follows (**11,** p. 254): Hypericineae 1, Erythroxyleae 2, Geraniaceae 2, Lythraceae 2, Rubiaceae 17, Primulaceae 3, Oleaceae 1, Gentianaceae 3, Polemoniaceae 1, Cordieae 1, Borragineae 1, Verbenaceae 1, Polygoneae 1, Thymeleae 1, and Pontederiaceae 1. The wide geographical distribution of the genera which contain heterostyled species and the fact that the families to which they belong are mostly very distinct from one another, indicate that heterostyly has arisen independently in several phylogenetic lines.

DARWIN considers (p. 245) that the morphological differences between the forms of a heterostyled species are confined to the flower. His observations on this point may be summed up briefly as follows: In the calyx there are no differences. The corolla

shows slight differences in shape due to the different position of the anthers. In *Pulmonaria* there is also a slight difference in the size of the corolla, and in *Pontederia* in its color. The most striking differences, of course, occur in the stamens and pistils (p. 247). The pistils differ in length of style and in size and shape of stigma. The stamens show a corresponding difference in length of filament or in place of insertion; and there is sometimes a difference in the color and thickness of the filaments, and in the size of the anthers. The pollen grains usually show a marked difference in size in the different forms. Of 43 cases cited, only 8 showed pollen grains of equal size in the different forms. In all the others the size of the pollen in the short-styled form exceeded that of the long-styled form (p. 249). The greatest difference was found in a trimorphous species of *Pontederia*, in which the diameters of the pollen grains from the longest stamens are to those of the shortest as 100:55, indicating a difference in contents in the ratio of 6:1.

These morphological differences are slight, however, compared with the physiological differences which accompany them. Repeated experiments have shown that complete fertility in heterostylous plants is secured only when a flower is pollinated with pollen from a flower of another form, that is, the pollen must come from a stamen equal in length to the pistil on which it is placed. The superiority of legitimate over illegitimate pollination is shown by the proportion of flowers which yield capsules and by the average number of seeds per capsule (p. 245). As DARWIN himself states, morphological characters alone do not furnish conclusive evidence of heterostyly. Final proof can be derived only from experiments which show that pollen must be applied from one form to the other in order to insure complete fertility.

The physiological difference in the forms is exhibited also in the time necessary to secure fertilization with legitimate and illegitimate pollen. DARWIN (p. 31) placed on several stigmas of a long-styled cowslip plenty of pollen from the same plant, and after 24 hours added some from a short-styled dark red polyanthus. From the flowers thus treated, 30 seedlings were raised, and all, without exception, bore reddish flowers. DARWIN describes a still more striking difference in *Linum perenne* (p. 87). He placed pollen

from a long-styled flower on all 5 stigmas of a long-styled flower on a separate plant. After 19 hours the stigmas were dissected and only a single pollen grain had emitted a tube. The pollen proved to be good when placed on the stigma of a short-styled plant. This experiment was repeated three times, with uniform results. A similar condition has been shown to occur in *Lythrum Salicaria* by STRASBURGER (**34**, p. 82). In this plant illegitimate pollination resulted in only a very slight growth of the pollen tube.

Physiological differences appear also in ways which less directly affect fertilization. In the long-styled form of *Linum perenne* (DARWIN, **11**, p. 130), each separate stigma rotates on its own axis when the flower is mature, thus turning its papillose surface outward. This movement is confined to the long-styled form. In *Faramea* the stamens of the short-styled form rotate on their axes. No such motion is found in the stamens of the long-styled form.

DARWIN'S experiments on the inheritance of heterostyly, like those of the other earlier workers, do not give very uniform results. But he deduces the general laws that seeds from illegitimate unions tend to reproduce the parent form (p. 271), and that illegitimate unions of long-styled plants tend to transmit the parent form more truly than do those of short-styled plants.

Recently, BATESON and GREGORY (**2**) have experimented on the inheritance of heterostyly in *Primula*. They find that in *Primula sinensis* the inheritance follows the Mendelian type, the short style being the dominant character and the long style the recessive. Short-styled plants are then heterozygotes, and half their gametes bear the dominant character, the other half the recessive; while long-styled plants are homozygotes and all their gametes bear the recessive character. One remarkable exception, however, was found. This was a single short-styled plant in which the female gametes were normal, that is, half bore the dominant and half the recessive character, while the male gametes bore the dominant character almost exclusively. BATESON and GREGORY note, as did DARWIN, that about half the eggs are fertilized by illegitimate pollen, while the rest are not; and suggest that this may be due to a differentiation of the egg cells of the plants.

ERRERA (**13**) has pointed out that *Primula elatior* shows what

he calls "caractères hétérostyliques secondaires." That is, the two forms differ not only in the parts of the flower, but also in the forms of the leaves. As he describes them (p. 229), the leaves of the long-styled form are "relatively longer and narrower, the ratio of the mean length (measured from the base of the petiole to the tip of the blade) to the maximum width being 2.86:1, and in plants grown in deep shade, 3.63:1"; while the leaves of the short-styled form are "relatively wider and shorter, the ratio of the mean length to the maximum width being 2.41:1, and in plants grown in the shade, 3.11:1."

Relation of heterostyly to dioeciousness

Dimorphic heterostylous plants present, in several respects, a striking resemblance to dioecious forms. In other hermaphrodite plants and in hermaphrodite animals, there is presumably unlimited possibility of crossing. In dimorphic heterostyled plants, however, the individuals are divided into two classes, which exist in approximately equal numbers and are adapted for reciprocal fertilization, a condition essentially the same as that found in dioecious plants and in the higher animals. This resemblance is made still more evident by ERRERA'S recent discovery of differences in the vegetative organs of the two forms in *Primula elatior*, comparable to the secondary sexual characters common in animals and found in a few dioecious plants, such as the hemp.

Naturally, no very definite comparison can be drawn between the inheritance of heterostyly and the inheritance of sex until it is decided what laws the inheritance of sex actually follows. But it may at least be pointed out that the condition described by BATESON and GREGORY for *Primula sinensis*, in which one form is a heterozygous dominant and the other a homozygous recessive, is exactly the condition believed, by several workers, to exist in the inheritance of sex, notably by CORRENS (**4**) for the dioecious *Bryonia alba*, and by BATESON for animals (Wilson **40**, p. 63). Aside from any analogy with dioecious plants, the work of BATESON and GREGORY on *Primula sinensis* indicates that in this form, at least, the inheritance follows the Mendelian law, a condition which indicates that a segregation of different characters occurs in the

reduction division of both megaspores and microspores of one form, in this case the short-styled form. Whether this is accompanied by any morphological difference in the chromosomes or not is of course another question.

The resemblance of dimorphic heterostylous plants to dioecious plants suggested to DARWIN (p. 285) that heterostyly may have been one of the ways by which the dioecious condition among flowering plants was attained. He cites several cases of plants which are dioecious, but show indications of a heterostylous ancestry. *Asperula scoparia*, an inhabitant of Tasmania, is dioecious, but the male flowers have large anthers and a very small pistil with rudimentary stigma and style, while the female flowers have a large, well-developed ovary and rudimentary anthers apparently quite destitute of pollen. *Discospermum*, of Ceylon, is apparently heterostyled, but one of the two forms is always barren, the ovary containing about two aborted ovules in each loculus, while in the other form each loculus contains several perfect ovules. The species is therefore really dioecious. Most of the species of the South American genus *Aegiphila* are heterostyled. In *Aegiphila obdurata*, however, the anthers of the long-styled form are entirely destitute of pollen, while the pistil is perfectly developed; in the short-styled form, on the other hand, the pistil is aborted, while the stamens are perfect.

There are a number of facts which indicate (BLAKESLEE **3,** p. 371) that in all dioecious plants one sex is dominant and makes its appearance while the other remains latent. Male and female willow plants are frequently found with flowers of the opposite sex. *Lychnis dioica* is normally dioecious, but STRASBURGER (**35,** p. 692) found in his cultures at Bonn occasional hermaphrodite plants. These were in every case affected by a smut, *Ustilago violacea*, and he attributes the hermaphrodite condition to the action of the fungus. *Ustilago violacea* fruits only in the anthers of the host plant. If it attacks a male plant it fruits in the anthers, and if it attacks a female plant, in some way it stimulates its host to the production of stamens, in which it fruits.

Recently SHULL (**32,** p. 112) has described occasional hermaphrodite plants occurring in a pure bred normal race of *Lychnis*,

in which *Ustilago violacea* has never appeared. He reverses (p. 119) STRASBURGER's interpretation of the origin of the diseased hermaphrodites, and suggests that the infected plants were males in which the disease allowed the pistils to develop. SHULL's discovery that hermaphrodite plants arise occasionally in normal races and his criticism of STRASBURGER's interpretations do not alter the importance of the fact that in a normally dioecious plant the bisexual condition may sometimes occur, perhaps because of some pathological stimulation. Another instance of the same condition is cited by STRASBURGER (**38,** p. 471). He reports, in the normally dioecious *Mercurialis annua*, male plants bearing a few female flowers, some of which when pollinated produced good seed.

The condition just described would seem to indicate that dioecious plants arose from the hermaphrodite condition. If such is the case, dimorphic heterostylous plants, since they already exist in two classes, which differ considerably and are adapted for reciprocal fertilization, might be more likely to become dioecious than would homostylous plants.

In this connection it is tempting to extend LILLIE's view of the origin of sex to the origin of dioeciousness in the higher plants. He assumes (**23,** p. 375) that fertilization may be always selective, even when there is no morphological gametic differentiation. According to his idea, gametes may be physiologically different even when they are morphologically alike. Morphological differentiation would then follow naturally, as the expression of these physiological differences, and sex differentiation as a further stage in the same process of evolution.

Is it not entirely probable that different "strains" may exist in some species of hermaphrodite plants which differ in their relations of fertility somewhat as do the different "forms" of heterostylous plants? Panmixia has always been assumed to be the natural condition of hermaphrodite species. That is, it has been assumed that any individual can fertilize or be fertilized by any other individual in the species with equal ease, but that such is actually the case has never been proven. The existence of different "strains" having such relations as suggested above would not be easily demonstrated under natural conditions, as each stigma

doubtless receives pollen from several flowers, among which it could easily "select" the favorable pollen, by inducing a more rapid growth of the pollen tube of the "legitimate" kind, exactly the method by which illegitimate fertilization is prevented, under normal conditions, in heterostylous plants.

The morphological differences shown by the different forms of heterostylous plants are really very slight compared with their physiological differences. According to the view suggested above, dimorphism, trimorphism, and dioeciousness would be merely morphological expressions of physiological differences common to many plants. Such an hypothesis would account for the origin of dioeciousness and heterostyly at different points, widely separated both geographically and genetically throughout the plant kingdom.

Fagopyrum esculentum

The dimorphous flowers of the buckwheat were first described and very accurately figured by HERMANN MÜLLER (**28,** p. 165; also **29,** p. 509). As MÜLLER points out, there are "in each form 8 stamens, 3 closely surrounding the styles and opening outwards, the 5 others inserted more outwards and opening inwards." The place occupied in one of the forms by the anthers is occupied in the other by the stigmas, a perfect adaptation for cross pollination by the numerous insects which visit the flowers for the sake of the honey secreted by the 8 globular nectaries at the base of the filaments. There is apparently no difference in the structure of the stigmas in the two forms, but the pollen grains of the short-styled form are larger than those of the long-styled form, their diameters being in about the ratio 5:4. There appear to be no secondary differences in the vegetative structure of the plants.

The flowers are as a rule true to form, and there is no difficulty in distinguishing long-styled from short-styled plants. Occasional flowers with the stigmas at the anther level, however, are seen on normal long-styled plants. Seldom more than one such flower occurs on a plant and this is usually the first which opens. A similar condition has been noted by BATESON and GREGORY in *Primula* (**2,** p. 583). One plant, however, was noted among some grown

for experimental purposes in the greenhouse, which showed such unusual floral variations as to be worthy of record. The plant produced 10 blossoms, and 8 of these had stamens and pistil both long; while 2, the third and eighth, were normal short-styled flowers. The earlier blossoms were removed in order to secure continued flowering. Later, however, two of the abnormal flowers were pollinated, one with pollen from a short-styled and the other with pollen from a long-styled flower, but neither developed seed. One of the normal short-styled flowers on this plant, however, produced a good seed when self-pollinated.

It will be noted that in both the cases cited above, in which the stamens and pistil are of the same length, it is the pistil which has varied from its normal length. That is, if a flower on a short-styled plant shows pistils and stamens of equal length, both are long; while in such a flower on a long-styled plant, both pistil and stamens are short. A curious case which shows a similar variation in the length of the pistil has been noted by BATESON and GREGORY (**2,** p. 583) in *Primula sinensis*. There is a variety with a very large yellow "eye" extending up over the limb of the corolla, quite distinct from the small yellow pentagon characteristic of the normal flower. This variety has the anthers in the position normal for long-styled plants, but the style is short and the stigma just reaches the anther level, a condition which BATESON and GREGORY designate as "equal-styled." In investigating the inheritance of these two unusual characters, they find that the "equal-style" is the form which the long-styled type assumes when the plant is homozygous in the large eye character. In this case, as in the others mentioned, the pistil alone varies from the normal length.

DARWIN experimented in a rather imperfect manner on the relative fertility of the two forms in the buckwheat, and showed that illegitimate fertilization is less successful than legitimate, yielding fewer and smaller seeds. In order to gain some knowledge of the relative ease of legitimate and illegitimate fertilization, the following experiment was made. Plants were grown from seed in a greenhouse, where there were no insects which might bring about pollination. The flowers which were to be experimented upon were examined with a lens in order to make sure that the pistils

had not been accidentally pollinated, and were castrated to prevent self-pollination. They were then pollinated artificially, either with pollen from a plant of the other form "legitimately," or with pollen from another plant of the same form "illegitimately."

After a definite number of hours, the pistils were fixed and microtone sections prepared. In the case of legitimate pollination, pistils fixed 18 hours after pollination showed regularly a 3-celled pro-embryo, and at least three free nuclear divisions had occurred in the endosperm. The embryo was usually in the quadrant stage 24 hours after legitimate pollination. The time elapsing between pollination and fertilization seems to have no relation to the distance traveled by the pollen tube, for it did not differ perceptibly in the two forms.

Pistils which had been illegitimately pollinated showed when sectioned that in 24 hours the pollen tube had made but a very slight growth. After 48 hours there was a greater development of the pollen tube; and in 3 days (72 hours) a few pistils showed the pollen tube extending nearly to the egg. Some of the pistils which were fixed 96 hours after illegitimate pollination showed the embryo in the 8- or 16-celled stage.

Under the conditions of the experiment then, if pollen from either form was placed on the stigma of a flower of the other form, the growth of the pollen tube and the fusion of the two nuclei required considerably less than 18 hours. But if pollen from either form was placed on the stigma of a flower of the same form, even though on a different plant, a period longer than 3 days was required for the tube to reach the egg. Illegitimate fertilization would then practically never occur in nature, especially in a form so frequently visited by insects. H. MÜLLER records (**28,** p. 165) 41 species of insects seen on the flowers of the buckwheat, many of them very frequently.

It is entirely possible that the rate of growth of the pollen tube was more rapid under the conditions of the experiment than it is in nature, for the temperature of the greenhouse in which the plants were grown was rather high. It does not seem probable, however, that this would affect the relative rate of growth of the pollen tube in the two cases.

THE REDUCTION DIVISION OF THE POLLEN MOTHER CELLS

Each loculus contains usually a single row of 8 or 10 pollen mother cells. All the cells of each loculus apparently pass through the different stages simultaneously, and there is no evidence of a regular basipetal succession in their development, such as has been reported in numerous cases. It was necessary, therefore, in order to determine the succession of the various stages, to compare carefully the cells of different loculi, using their size and the condition of their cytoplasm as a check upon the order of the phases shown by the nuclei. Considerable variation in different loculi of the same flower is common.

PROPHASE.—The pollen mother cells first become distinguishable by their increased size and the possession of a large nucleus, containing a single large, dark staining nucleolus (figs. 1, 2). This nucleolus is surrounded by a clear zone which is apparently not affected by any of the stains used. In a few cases two such nucleoli were observed in one nucleus, each surrounded by the colorless area just described. The nature of this clear space seems to be rather uncertain. It has been figured frequently, and is regarded by some writers as a constant structure. MARTINS MANO (**24,** p. 60) speaks of it as the "peri-nucleolar vacuole." STRASBURGER, however, considers that the appearance is due to reagents (**37,** p. 519).

Surrounding this clear zone is the nuclear reticulum, consisting of very delicate indefinite threads which do not take the chromatin stain. This "linin" network contains scattered dark staining bodies which are apparently rather irregular in number and do not seem to occur in pairs. They thus furnish no support for the attractive prochromosome theory of ROSENBERG (**31,** p. 25) and others.

SYNAPSIS.—The recent work of LAWSON (**22**) has again raised the question as to whether the phase of the nucleus preceding the reduction division, characterized by an apparent condensation and contraction of the chromatin on one side of the nuclear cavity, is a real contraction. For some time this condition was regarded as an artifact, but it has been observed in living material by several investigators, and its occurrence, at least in some forms, is now

generally admitted. Some writers, however, still regard it as due to imperfect fixation.[1] This stage was first called "synapsis" by MOORE in 1895; and many cytologists have come to regard it as an important and critical stage, when the actual fusion of the maternal and paternal chromosomes occurs.

LAWSON presents a different explanation of the condition observed. He interprets the phenomenon as simply a growth period of the nucleus, during which the increased osmotic pressure within the nucleus causes the absorption of a considerable amount of cell-sap, and the consequent increase in size of the nucleus. In this enlargement the chromatin mass is left behind. The characteristic position of the chromatin mass at one side of the nucleus, according to LAWSON, is due to the fact that the extension of the nuclear cavity always takes place in one direction, that is, on the side toward an intercellular space where there is least resistance from the neighboring cells.

Since the publication of LAWSON's paper, the writer has studied the synaptic stages in the buckwheat with special reference to the comparative size of the nucleus and chromatin mass before and during synapsis. There is certainly an increase in the size of the nucleus during the synaptic stages, as will appear from a comparison of figs. 3, 4, and 5. It seems equally certain that the chromatin mass occupies a much smaller space during the "balled-up" condition than it does either before or after this stage. The stage is evidently of considerable duration, longer than all the later stages in the heterotypic division combined.

It is of course possible that the contraction is due to imperfect fixation, that the nuclear matter is for some time in such a condition that it is impossible to preserve its structure by any known method. A contraction at this stage, however, is of constant occurrence, and the chromatic material has a characteristic appearance after the "contraction" which differs markedly from its appearance before. The same conditions were found in *Houstonia;* and in the following descriptions it will be assumed that synapsis is a normal stage.

A comparison of the nuclei before and after synapsis is rendered

[1] A full discussion of this subject, together with citations of literature, is given by GRÉGOIRE (**17**, pp. 332–335).

easier by a change which takes place in the cell at this time, and by which postsynaptic stages are clearly distinguished from presynaptic stages. During the contracted condition of the chromatic mass the pollen mother cell becomes rounded and takes on a more spherical form. In figs. 3, 4, and 5, the nuclei are apparently in much the same stage, but the cells show a progressive "rounding off." Such a change in the shape of the cell during synapsis has been observed by STRASBURGER, ALLEN (**1,** fig. 19), DAVIS (**12,** p. 634), and others, and appears in the figures of many workers who make no particular mention of it.

The synaptic contraction seems to take place by a drawing together, at one side of the nucleus, of the whole nuclear reticulum, usually but not always including the nucleolus (figs. 3 and 5). On careful examination this mass appears to consist, at least in part, of delicate threads; but no evidence of any pairing of these threads, such as has been described by some investigators, could be obtained. The threads of the nuclear reticulum in the buckwheat are so delicate, however, that it would be extremely difficult to demonstrate any such condition even if it occurred; and the behavior of the chromatin at later stages makes it seem probable that a pairing has actually taken place at this stage.

The amount of chromatin staining material is very markedly increased during synapsis. Before the contraction, the greater part of the reticulum does not take the chromatin stain; but the nuclear mass comes out of the contracted condition as a series of rather thin loops (fig. 7), each of which consists, apparently, of a single thread which takes the chromatin stain uniformly throughout its length. This thread is granular in appearance and varies somewhat in thickness; but no alternation of chromatic and achromatic material, such as has been described by some writers at this stage, could be made out. The number of loops is rather inconstant, but is generally greater than the number of gemini.

These loops gradually shorten and thicken (fig. 8) and become more dense and uniform in appearance. At the time of greatest thickness they undergo a longitudinal split (fig. 9), thus giving rise to a series of paired chromatic threads from which the gemini are apparently formed by the continued gathering together of the

chromatic material. The stages from the loosening of the synaptic knot to the formation of the gemini are passed through rather rapidly; and the changes apparently take place in all parts of the nucleus at practically the same time. There does not seem to be any definite "second contraction," but rather a continuous shortening and thickening of the threads from the time the thin loops first appear until the gemini are formed.

The two members of a geminus are generally united at one end, but they are often found entirely separate or united throughout their length (figs. 11 and 12). Their appearance in figs. 10 and 11 would indicate that the loops from which they arose consisted of both chromatin and linin, and that in the formation of gemini at least a part of the linin is discarded. Diakinesis is apparently of considerable duration and affords an excellent opportunity for counting the chromosomes. The reduced number is evidently 8. The nucleolus appears at this stage as a pale and somewhat irregular body (figs. 10–12).

The succeeding stages present no unusual features. The first division separates the two members of the gemini, but there is no evidence of a longitudinal split in the chromosomes during the anaphase (fig. 13). During interkinesis the daughter nuclei of the first division approximate somewhat a resting condition. A rather definite nuclear membrane is formed, a pale nucleolus appears, the chromosomes become more or less vacuolate, and are connected to some extent by indefinite linin threads (fig. 18). It is usually possible at this stage, however, to make out the separate chromosomes and to determine definitely the reduced number, 8. The second division is a typical homotypic division.

It will be noted that the condition described for the buckwheat corresponds closely with the "hétérohoméotypique scheme" of GRÉGOIRE (**17,** p. 233). His "scheme" may be briefly outlined as follows: In the early prophase (p. 243) of the reduction division, the nuclear mass becomes resolved into a number of fine threads, each of which is the equivalent of a somatic chromosome. This is the leptotène stage. These threads, the "gamomites," become arranged in pairs (zygotène stage), which afterward fuse to form a series of independent loops, the pachytène loops. These pachy-

tène loops exist in the haploid number, and soon undergo a longitudinal division, which is really the separation of the parts which united in their formation. The halves thus separated often appear irregularly spread apart and crossed, the "strepsitène" stage; and the "gemini" are formed by the shortening and thickening of these strepsitène loops. Diakinesis (p. 232) is characterized by the presence of "chromosomes" in the reduced or haploid number, formed often of two rather independent branches. The first division separates the two branches of these "chromosomes," and the daughter chromosomes show during the anaphase of the first division a longitudinal split, which is sometimes visible in the two branches of the diakinetic "chromosomes." After an interkinesis, more or less brief, marked by varying degrees of nuclear reconstruction, the daughter chromosomes of the first division reappear, and their longitudinal halves are separated in the second division.

In GRÉGOIRE'S scheme, synapsis, when it occurs, is due to the contraction which accompanies the fusion, in pairs, of the leptotène threads to form the pachytène loops. If this change takes place simultaneously throughout the nucleus, a crowding of the whole chromatin mass at one side is the result.

If it is assumed, as seems probable, that in the buckwheat a fusion of thin filaments takes place in the presynaptic stages, then the series of loops characteristic of the early postsynaptic period represents a pachytène stage. There are, however, considerably more than the haploid number of loops. This may mean either that the loops representing the chromosomes are long (GRÉGOIRE, p. 335) or that they are parts of a continuous spirem thread. These two explanations represent the two interpretations of the spirem condition, STRASBURGER and his school maintaining that the chromatic mass comes out of synapsis as a continuous spirem thread, GRÉGOIRE holding that the so-called spirem is really a series of independent loops. On this point the buckwheat furnishes no evidence. It seems certain, however, that these loops become shortened and thickened and undergo a longitudinal split, forming the strepsitène loops, from which the gemini are derived by a continued thickening.

It was also noted above that no split in the chromosomes is evident in the anaphase of the first division. But though such a split is stated by GRÉGOIRE to be a part of his "scheme," its absence cannot be regarded as a very important deviation.

THE CHROMOSOMES IN THE REDUCTION DIVISION

As the chromosomes become vacuolate during interkinesis, the stage most favorable for an examination and comparison of the chromosomes is the anaphase of the reduction division (fig. 13). The most striking thing about the chromosomes at this stage is their different size in the two forms. The chromosomes of the short-styled form have a diameter nearly twice as great as do those of the long-styled form (compare figs. 14 and 15 with figs. 16 and 17). As it is entirely improbable that this difference in size can be due to any difference in the hereditary qualities borne by the two sets of chromosomes, it appears to be related with the corresponding, though smaller, difference in the size of the microspore mother cells at this stage.

Just what relation exists between the size of the cell, the size of the nucleus, and the size and mass of the chromosomes is not well understood. There seems, at any rate, to be no definite relation between the number of chromosomes and the size of the nucleus. STRASBURGER (**36,** p. 51) cites several cases in which the nuclei with the diploid number of chromosomes are distinctly larger than those with the haploid number in the same species. In the seed rudiments of *Taxus baccata*, for example, the nuclei of the prothallium are much smaller than those of the nucellus. That the diploid number of chromosomes is not always associated with a larger nucleus than that which contains the haploid number, however, he proves by the case of *Dictyota dichotoma*, in which species the nuclei of the plants which produce tetraspores are no larger than those of the plants which bear eggs or sperms, though they have, of course, twice as many chromosomes.

Another difference between the two forms, which is apparently constant, is the arrangement of the chromosomes in the anaphase of the heterotypic division. In the short-styled form the eight chromosomes tend to be arranged with six in the peripheral ring

and two in the middle; while in the long form the arrangement shows seven in the periphery and one in the middle. This arrangement may of course be accidental or it may be mechanical, due to the difference in the chromosomes (compare figs. 14 and 15 with figs. 16 and 17).

A careful examination of the cells in the late anaphase of the heterotypic division of the short-styled form failed to show any difference in the chromosomes (figs. 14 and 15). In the long-styled form, however, the "central" chromosome is apparently considerably larger in one of the daughter nuclei of the heterotypic mitosis than is its synaptic mate in the sister nucleus (figs. 16 and 17). While this condition is apparently constant, little importance can be attached to it until more is known of the inheritance of heterostyly in the buckwheat,[2] and of the reduction division of the megaspores. It bears a striking resemblance, however, to the condition found in the sperm mother cells of *Lygaeus* and other insects (WILSON, **40,** p. 59) in which there is an "*x*" chromosome which has as a synaptic mate a smaller "*y*" chromosome.

GROWTH OF THE POLLEN MOTHER CELLS

The difference in the size of the pollen grains of the two forms has been referred to above. As a corresponding difference in size was apparent in the pollen mother cells during early stages, an examination was made to determine whether a similar difference in size occurs in the somatic cells. Buckwheat seeds were allowed to germinate on moist filter paper, and when the roots were about half an inch in length the tips were removed with a sharp razor and fixed at once. Seeds and root tips were carefully marked to correspond and the seeds planted.

The seedlings developed readily, and when the plants blossomed, microtome sections of the root tips were prepared and the size of the embryonic cells of the two forms compared. The cells measured, of course, were always in the same stage, usually the metaphase. Some variation in the size of the embryonic cells even in the same stage was noted, but no constant difference between the two forms

[2] DARWIN's experiments on this species, as he himself states, were very imperfect, and gave the result that illegitimate seeds of either form produced plants of both forms.

could be demonstrated. No difference is apparent either in the resting nuclei of the pollen mother cells or in the pollen mother cells themselves (figs. 1 and 2). The difference becomes evident, however, after the rounding off of the pollen mother cells during synapsis, and apparently reaches its maximum some time before diakinesis, (compare figs. 7 and 8; and figs. 11 and 12). It is of course much easier to measure accurately spherical cells than angular cells massed together, as it is extremely difficult to determine in the latter case whether the cells are cut in the same plane or not, and there may be a difference in the size of the somatic cells which could not be determined. It seems entirely probable, however, that the difference in the size of the pollen of the two forms is due to the fact that the pollen mother cells of the short-styled form grow more rapidly during the period from the beginning of synapsis to diakinesis, than do the microspore mother cells of the long-styled form. It is interesting to note in this connection that it is during this same period that the ovocyte in animals undergoes its greatest enlargement (GRÉGOIRE, **17**, p. 243).

SEPARATION OF THE POLLEN GRAINS

The separation of the pollen grains occurs in much the same way as was described by Miss FERGUSON for *Pinus* (**14**, p. 35). During the late telophase of the second mitosis in the microspore mother cell the four nuclei of the tetrad become connected with one another in all directions by "kinoplasmic" fibers (fig. 19). These fibers, however, are never very numerous, and they are visible for only a comparatively short time after the reconstruction of the daughter nuclei is complete. During this period a marked thickening of the wall of the pollen mother cell occurs (fig. 20); and, apparently continuous with this wall and extending out from it, walls appear separating the daughter cells (fig. 21).

These walls attain a remarkable thickness, and are apparently homogeneous and extremely resistant to stains. They stain very lightly with haematoxylin or safranin, and with orange G only if the staining be considerably prolonged. The strength and definiteness of the walls thus formed is shown by the fact that after the spores are mature and the wall of the mother cell is ruptured, the

empty mother cell wall with its four chambers often persists for some time (fig. 22).

TAPETAL CELLS

About the time the pollen mother cells reach the pachytène stage, the tapetal cells begin a rather irregular free nuclear division. The nuclei show all gradations from true mitosis to what is apparently simple amitotic division. Figs. 23–25 show the amitotic division of these nuclei. By the time the pollen mother cells have finished the homotypic division, the tapetal cells regularly contain two and sometimes four free nuclei (fig. 26).

MEGASPORE MOTHER CELLS

The difficulty of orienting the buds makes the number of preparations necessary to secure a full series of stages so great that a complete study of the development of the megaspores has not yet been made. One preparation of the long-styled form, however, showed typical diakinesis, which, as was to be expected, had much the same appearance as that in the microspore (fig. 27). Usually only one megaspore mother cell is formed in an ovule, and each flower produces but a single seed. One ovule, however, which happened to be in the long-styled form, contained two apparently well-developed and normal megaspore mother cells, with their nuclei in the pachytène stage. Their shape seems to indicate that they were formed by the division of a single cell by an anticlinal wall (fig. 28).

Houstonia caerulea

The Rubiaceae contain nearly half the genera known to be heterostylous. The flowers of *Houstonia* are plainly dimorphic, the pistil being exserted in one form and the stamens in the other. The pollen grains vary somewhat in size in each form, but those of the short-styled form are larger than those of the long-styled, their diameters being in about the ratio 10:7. No differences have been noted in the vegetative structures of the two forms. The flowers are so small that experimenting with them would be very difficult, and accordingly very little is known about the relative fertility of legitimate and illegitimate unions. DARWIN, however (**11**, p. 132),

observed that some short-styled plants growing by themselves at a considerable distance from any long-styled plants produced mostly sterile capsules. From this he concludes that the short-styled form is very sterile with it own pollen.

The pollen mother cells are small and a large number are contained in one loculus, often as many as 40 appearing in a single longitudinal section. Considerable variation is generally shown by the cells of a loculus, but there does not seem to be any very regular succession of stages. Frequently, to be sure, an anther shows a progressive series with the most advanced stages at the top; but this is by no means a uniform condition, for occasionally a loculus shows the mother cells near the middle in a more advanced condition than the cells at either end. The relative position of the cells in an anther does not, then, in *Houstonia*, furnish reliable evidence of the succession of the stages. This makes the exact significance of some stages rather uncertain, and some of them are open to more than one interpretation.

THE REDUCTION DIVISION OF THE POLLEN MOTHER CELLS

PROPHASE.—The pollen mother cells first become distinguishable by their increased size and the possession of a very large nucleus. The nuclear reticulum appears as a network of very fine irregular threads, and contains numerous granules, none of which take the chromatin stain. There is usually only a single large nucleolus, and this is surrounded by the clear zone already described in the buckwheat.

The nuclei of the pollen mother cells present at this stage an appearance which has been variously interpreted. Figs. 29–33 show what appears like a progressive "budding off" of chromatin staining material from the nucleolus. A similar condition has been observed by DARLING (**5,** p. 184) in *Acer Negundo*, and described as a budding off of actual chromatin which goes to make up the spirem thread. Miss NICHOLS (**30,** p. 35) has observed this condition in *Sarracenia*, and considers that it represents a movement of chromatin, which has been elaborated in the nucleolus, to the nuclear reticulum. GATES (**15,** p. 6) interprets a similar appearance in *Oenothera* in an entirely different manner. He regards the

dark staining bodies in the nuclear reticulum as small nucleoli, and thinks that conditions similar to those in figs. 30, 32, and 33 represent a fusion of some of these smaller nucleoli with the large one.

As it is impossible to arrange these stages in *Houstonia* with any certainty, there is no proof as to what actually takes place. The appearance strongly suggests a "budding off" of material which is caught up by the nuclear reticulum; and the presence of numerous dark staining bodies in the reticulum at the time of synapsis (figs. 34 and 35) have been held to show that such is actually the case. There is no proof, however, that the dark staining bodies which are present in the reticulum at this time have any connection with the nucleolus. In fact, a series of somatic stages, taken from the rapidly growing tissue of a young ovule (figs. 36–42), seems to show that the dark staining masses appearing in the reticulum previous to the formation of the spindle have no connection, at least directly, with the spherical bodies observed near the nucleolus, but that they are chromosomes which become differentiated from the nuclear reticulum during the prophase.

SYNAPSIS.—Synapsis is characterized by a crowding together at one side of the nucleus of the entire nuclear reticulum (figs. 34 and 35). No structure can be made out in this mass except that it consists of a number of dark staining bodies in a much lighter, rather indefinite network. Synapsis is of considerable duration, and during this period the nucleus undergoes a marked increase in size (compare figs. 34 and 35) and the cell becomes rounded (fig. 43).

SPIREM STAGE.—The chromatic mass comes out of synapsis in a series of thin loops (figs. 43 and 44). Each loop apparently consists of a single thin thread which does not take the chromatic stains uniformly throughout its length, but shows numerous dark staining bodies, connected by paler linin portions. As these loops shorten and thicken they stain more uniformly (fig. 45).

The synaptic knot loosens very slowly, and even at the period of greatest thickening of the loops there is still a considerable portion of the nuclear mass, which does not show any definite structure, surrounding the nucleolus (fig. 45). This condition can be explained only on the supposition that some parts of the nucleus often pass

through the various stages in advance of others, a condition comparable to that noted by JANSSENS (**21**) in *Batracoseps*. The appearance at later stages seems to bear out this supposition. Fig. 46 shows a split in a portion of the spirem, while the rest appears entirely undivided. Fig. 47 shows several places where the parts have become still more widely separated, yet a considerable mass of the nuclear material is still in synapsis; and fig. 49 shows all gradations from paired loops to typical gemini.

This irregularity in development, together with the fact that there is no definite succession of stages in the loculi, makes a fully satisfactory interpretation of the spirem stages impossible. If it is true, however, as seems probable, that the chromatic loops which appear as the mass emerges from synapsis consist of a single thread[3] which afterward shortens and thickens, and if the split shown in figs. 46 and 47 represents a separation of threads previously paired, the series accords closely with GRÉGOIRE'S hétérohoméotypique scheme. Figs. 44 and 45 would then represent the pachytène stage, the loops shown in fig. 45 resulting from a shortening and thickening of thinner loops shown in fig. 44. Fig. 46 doubtless represents a splitting of the pachytène loops, the diplotène stage. Figs. 47 and 48 show different stages in strepsinema; in fig. 47 only a small part of the nuclear mass is in the strepsitène condition, while fig. 48 is a more advanced stage.

The appearance of fig. 43, which is quite characteristic of the loosening of the synaptic knot, makes it appear possible that the spirem comes out of synapsis as a series of paired threads which afterward fuse to form a continuous spirem. That this actually occurs in most cases is held by STRASBURGER and his school. Such a condition as is shown in fig. 44, however, where the loops appear still thin but with the halves widely separated, makes it seem probable that the thickened spirem arises from the thinner by a thickening of the threads. That is, figs. 44 and 45 represent merely different phases of the pachytène stage.

[3] In referring to this stage as characterized by the occurrence of loops consisting of a single thread, the writer does not mean to enter into the discussion as to whether this "single thread" is really a unit or is composed of two separate threads twisted together. The expression "single thread" is used to mean simply a loop which appears as one thread, as distinguished from one composed of two parallel threads.

DIAKINESIS.—In either case the diakinetic gemini arise by the continued shortening of the paired loops which make up the strepsitène stage. As shown by fig. 49, diakinesis may not arise simultaneously throughout the nucleus. The stage is of considerable duration, however, and presents a very characteristic appearance (figs. 50 and 51). The chromosomes of a geminus are generally united only at one end and often diverge widely from one another. The nucleolus at this stage appears vacuolate, and shows in section an outer dark staining region surrounding an inner almost colorless portion. Commonly at this stage one or two gemini appear clinging to the nucleolus (fig. 51). Their appearance suggests the condition reported by DARLING (**5,** p. 186) for *Acer Negundo*, where five chromosomes appear to arise directly from the nucleolus. There is nothing in *Houstonia*, however, to indicate that this condition is anything more than a clinging of the gemini to the nucleolus.

Another characteristic appearance during diakinesis is that shown in figs. 52 and 53, where several gemini appear clinging together in a single row. This condition very much resembles that found by GATES (**15,** p. 12) in *Oenothera*. GATES, however, considers that in *Oenothera* this condition is previous to true diakinesis, and represents a single continuous spirem constricted at regular intervals to form a chain of chromosomes. Some of these chromosomes afterward pair to form typical gemini, but a considerable number of them are apparently taken up by the heterotypic spindle without having previously paired. An essentially similar method of formation of the diakinetic chromosomes has been reported by GEERTS (**16,** p. 610) and by Davis (**12,** p. 559) for *Oenothera*, and by YAMANOUCHI (**41,** p. 186) for *Fucus*.

That such is the case in *Houstonia*, however, seems improbable, as such an interpretation makes it necessary to regard the condition shown in figs. 46 and 47 as a precocious split which afterward closes up. Moreover, the two members of each geminus in *Houstonia* are almost always found attached at one end, while in *Oenothera* such a condition is the exception. The condition shown in figs. 52 and 53 seem to be best explained as a temporary union of independent gemini, an interpretation first suggested by MIYAKE (**25,** p. 96) for a similar appearance in *Galtonia candicans*.

INTERKINESIS.—The heterotypic division presents no unusual features, but interkinesis differs markedly from that of the buckwheat. Although a rather definite nuclear membrane is formed, the chromosomes show no signs of vacuolation or anastomosis. On the contrary, they become arranged around the periphery of the nucleus and present at this stage the most satisfactory opportunity for counting and comparing the chromosomes (figs. 57 and 58). The haploid number is 16.

Nucleoli appear at this stage and stain with haematoxylin in exactly the same way as the chromosomes themselves; in fact they were at first mistaken for larger, more regular chromosomes. With safranin, however, the nucleoli are clearly differentiated from the chromosomes. There may be either one or two nucleoli at this stage, but sister nuclei seem to agree in this respect, that is, if one daughter nucleus of the first division shows one nucleolus, its sister nucleus also has only one, but both may, on the other hand, have two nucleoli (figs. 57 and 58). This peculiarity seemed at first to bear out the idea that they were chromosomes, and there seems to be a constant difference between the two forms, the long-styled form having two nucleoli (fig. 58) and the short-styled form one larger nucleolus (fig. 57). This may possibly be due to the different sizes of the nuclei in the two forms.

THE CHROMOSOMES IN THE REDUCTION DIVISION

Interkinesis, because the chromosomes remain apparently unchanged and are arranged in the periphery of the nucleus, affords the best opportunity for comparing the chromosomes of the reduction division. No difference in the chromosomes that enter into the formation of the daughter nuclei could be discovered. In fact, both in interkinesis and in the anaphase of the reduction division the chromosomes show very little variation in size. A constant difference in size between the chromosomes of the long-styled and short-styled forms is evident in the anaphase, but this is much less marked than in the buckwheat (compare figs. 55 and 56).

RELATIVE SIZE OF THE POLLEN MOTHER CELLS

The pollen grains of the two forms differ fully as much in size as do the two forms in the buckwheat, but the difference does not

seem to appear so early in their development. The fact that the cells are small and vary somewhat in size makes it difficult to determine when the difference becomes most pronounced; but it will be clear from a comparison of the figures that at diakinesis, the heterotypic division, and the formation of the tetrad, some difference in size is evident. Compare figs. 50 and 51, 55 and 56, and 59 and 60.

SEPARATION OF THE POLLEN GRAINS

The daughter nuclei of the homotypic division show at an early stage a nucleolus similar in staining reactions to that of interkinesis (figs. 59 and 60). That is, the nucleoli stain with hematoxylin exactly the same as the chromosomes, so that in early stages of nuclear formation it is impossible to distinguish them, and the nucleolus appears to arise by a fusion of the chromosomes. Staining with safranin, however, shows clearly that the nucleolus arises separately, but increases in size as the chromosomes lose their staining capacity.

The separation of the pollen grains takes place in much the same way as in the buckwheat, except that in *Houstonia* the "kinoplasmic" fibers connecting the nuclei of the tetrad are much more clearly marked and persistent. The walls which surround the mother cells and separate the cells of the tetrad are not so thick or resistant as in the buckwheat.

Summary of observations

Fagopyrum esculentum

The flowers, as a rule, are true to form, but occasional "equal-styled" flowers are found on both long-styled and short-styled plants. None of these "equal-styled" flowers have been proved to be fertile.

In the case of legitimate pollination less than 18 hours is required for the growth of the pollen tube and the fusion of the egg and sperm nuclei. Illegitimate fertilization is possible, at least in part of the cases; but in case of illegitimate pollination more than 72

hours is necessary for the growth of the pollen tube and the fusion of the nuclei.

No evidence of prochromosomes was found in the pollen mother cells.

The formation of the gemini and the reduction division apparently follow the hétérohoméotypique scheme of GRÉGOIRE; but no split in the chromosomes is evident in the anaphase of the first division.

The reduced chromosome number is 8.

In the anaphase of the reduction division of the microspore mother cells the chromosomes of the short-styled form have a diameter nearly twice as great as do those of the long-styled form.

At this stage the chromosomes of the short-styled form are arranged six in the peripheral ring and two in the middle; while those of the long-styled form are arranged seven in the periphery and one in the middle.

In the long-styled form the "central" chromosome of one of the daughter cells of the first division appears to be larger than its synaptic mate.

Interkinesis is characterized by a partial reconstruction of the nuclei, a nucleolus appears, and the chromosomes become somewhat vacuolate but never lose their identity.

A difference in size of the pollen mother cells of the two forms, corresponding to the difference in the size of the pollen grains, is evident at diakinesis. This difference apparently arises through the greater growth of the pollen mother cells of the short-styled form up to this stage, for no difference in the size of the somatic cells can be found.

At the separation of the cells of the tetrad a thick wall, apparently homogeneous and extremely resistant to stains, is formed surrounding the pollen mother cells and separating the pollen grains.

As the tapetal cells degenerate, they show free nuclear division which is to some extent at least amitotic.

Usually only one megaspore mother cell is formed in an ovule, but one ovule was found which showed two well-developed megaspore mother cells. These had apparently arisen by the longitudinal division of a single cell.

Houstonia caerulea

The nuclei and chromosomes of the pollen mother cells are so small that many of the prophasic phenomena could not be observed with accuracy, but the formation of the gemini and the reduction division seem to follow the "hétérohoméotypique scheme."

Some portions of the nuclei go through the postsynaptic changes in advance of others.

Diakinesis is characterized by a portion of the gemini arranging themselves end to end in a sort of chain.

The reduced chromosome number is 16.

During interkinesis the chromosomes apparently remain unchanged, and are arranged about the periphery of the nucleus. The nucleoli which appear at this stage resemble the chromosomes when stained with haematoxylin.

No difference is apparent in the chromosomes which separate in the heterotypic division.

In the anaphase of the reduction division the chromosomes of the short-styled form are slightly larger than those of the long-styled form.

The separation of the cells of the tetrad occurs in the same way as in the buckwheat.

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EXPLANATION OF PLATES XXI–XXIII

All figures ×1600

PLATE XXI

Microspore mother cells of *Fagopyrum esculentum*

FIG. 1.—Long-styled form: early prophase.

FIG. 2.—Short-styled form: same stage as fig. 1.

Figs. 3–5.—Long-styled form: successive stages in synapsis.

FIG. 6.—Short-styled form: same stage as fig. 5.

FIG. 7.—Short-styled form: early pachytène stage.

FIG. 8.—Long-styled form: later pachytène stage.

FIG. 9.—Long-styled form: strepsitène stage.

FIG. 10.—Long-styled form: gathering together of chromatic substance in the formation of gemini.

FIG. 11.—Short-styled form: diakinesis.

FIG. 12.—Long-styled form: diakinesis.

Figs. 13–15.—Short-styled form: anaphase of the reduction division.

Figs. 16, 17.—Long-styled form: anaphase of the reduction division.

Fig. 18.—Long-styled form: interkinesis.

PLATE XXII

Fagopyrum esculentum

Figs. 19–21.—Long-styled form: successive stages in the separation of the pollen grains.

Fig. 22.—Short-styled form: mother cell wall from which the pollen grains have fallen.

Figs. 23–26.—Long-styled form: tapetal cells showing successive stages in amitotic free nuclear division.

Fig. 27.—Long-styled form: megaspore mother cell; nucleus in diakinesis.

Fig. 28.—Long-styled form: two megaspore mother cells in a single ovule; nuclei in pachytène stage.

Houstonia caerulea

Figs. 29–33.—Long-styled form: microspore mother cells in early prophase.

Fig. 34.—Long-styled form: beginning of synaptic contraction.

Fig. 35.—Long-styled form: synapsis.

Figs. 36–42.—Somatic cells, showing successive stages in growth and division.

PLATE XXIII

Microspore mother cells of *Houstonia caerulea*

Fig. 43.—Long-styled form: loosening of the synaptic knot.

Figs. 44, 45.—Long-styled form: pachytène stage.

Fig. 46.—Long-styled form: tangential view of nucleus in diplotène stage.

Figs. 47, 48.—Long styled form: strepsitène stage.

Fig. 49.—Long-styled form: gemini in process of formation.

Fig. 50.—Short-styled form: diakinesis.

Figs. 51–53.—Long-styled form: diakinesis.

Fig. 54.—Short-styled form: anaphase of the heterotypic division.

Fig. 55.—Short-styled form: polar view of chromosomes in anaphase of heterotypic division.

Fig. 56.—Long-styled form: same stage as fig. 55.

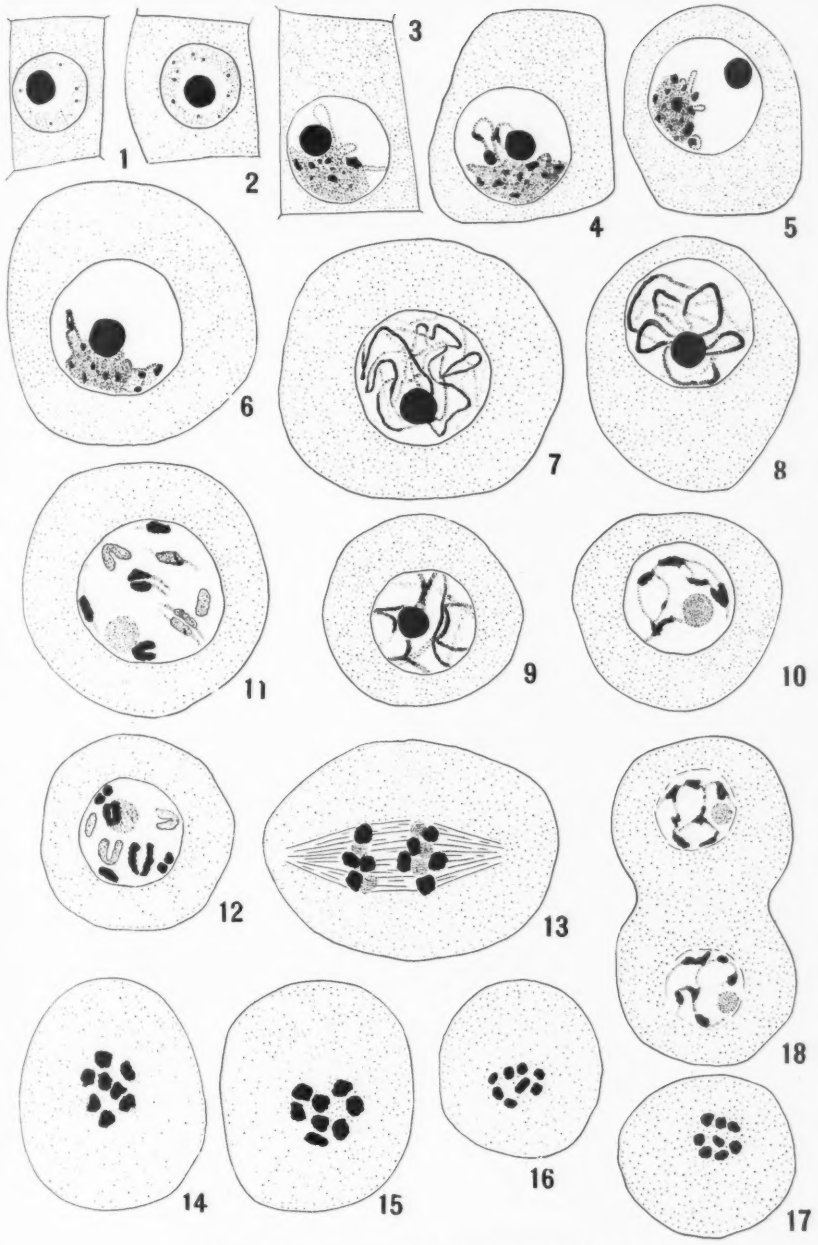
Fig. 58.—Long-styled form: interkinesis.

Fig. 57.—Short-styled form: interkinesis.

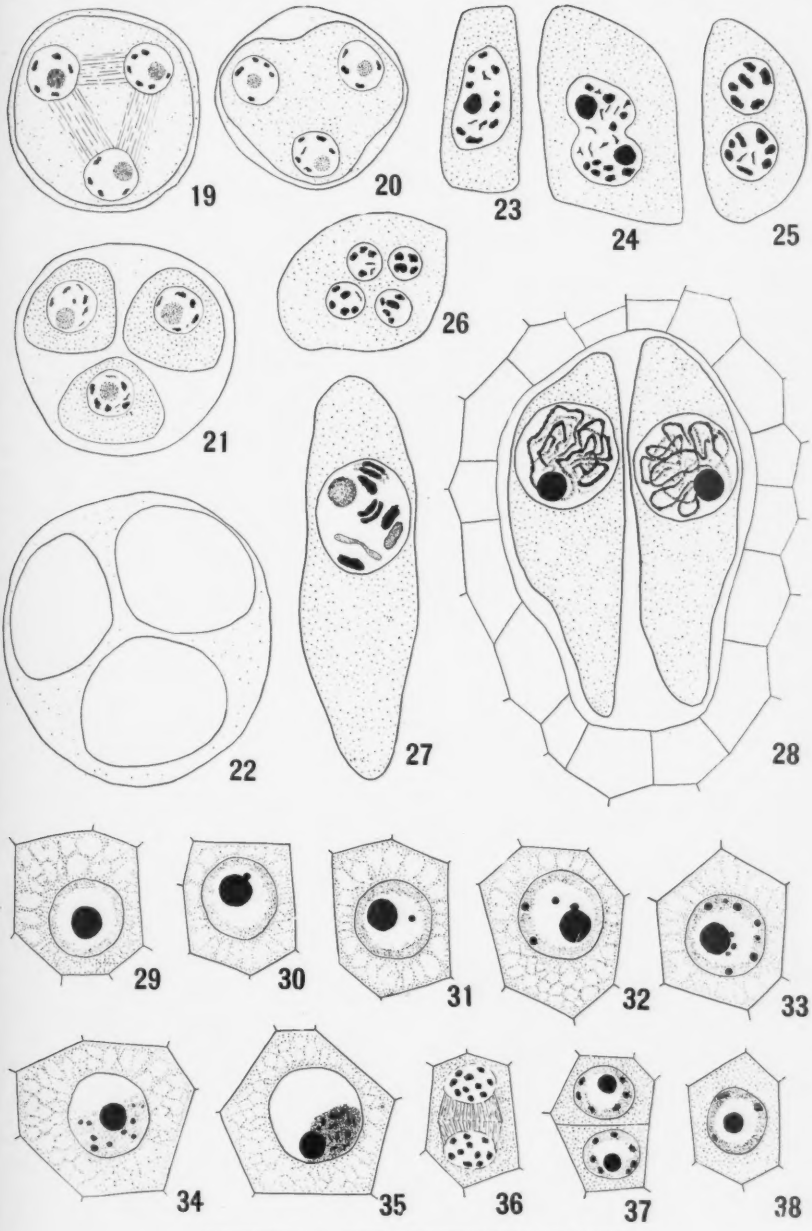
Fig. 59.—Long-styled form: reconstruction of daughter nuclei of the homotypic division.

Fig. 60.—Short-styled form: same as fig. 59.

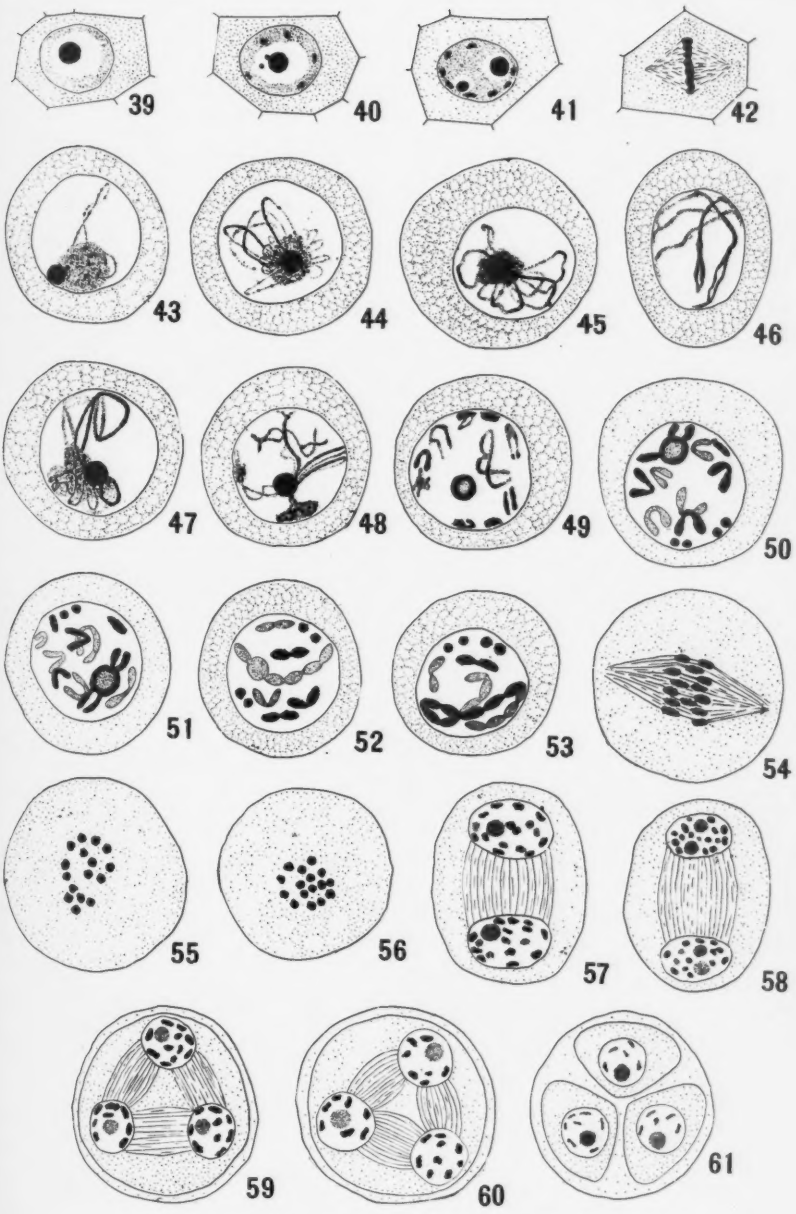
Fig. 61.—Long-styled form: separation of pollen grains.



STEVENS on HETEROSTYLOUS PLANTS



STEVENS on HETEROSTYLOUS PLANTS



STEVENS on HETEROSTYLOUS PLANTS

RELATION OF THE DAILY MARCH OF TRANSPIRATION TO VARIATIONS IN THE WATER CONTENT OF FOLIAGE LEAVES

BURTON EDWARD LIVINGSTON AND WILLIAM HENRY BROWN[1]

Introduction

As was first pointed out in Publication 50 of the Carnegie Institution (1906), it is only by correcting the variations in the transpiration rate to uniform conditions of evaporation (that is, to a uniform evaporating power of the air), that anything approaching quantitative information concerning the seemingly almost autonomous changes in the rate of water loss from plants may be had. To accomplish this correction it is only necessary to consider the march of the ratio of the rate of transpiration to that of evaporation, the latter determined by means of some form of atmometer. This ratio has been termed *relative transpiration;* it denotes simply *the number of atmometers of the form used that would be necessary to evaporate the same amount of water as is lost by the transpiring plant in the same time and at the same place.* In other terms, relative transpiration is a measure of the equivalent or effective evaporating surface of the plant as this varies from time to time, the unit of evaporating surface being unit area of free water surface under properly defined conditions, or any other evaporating surface which may be adequately defined.

Reference to the nine graphs of relative transpiration presented in the publication just mentioned, and to the accompanying discussions, brings out the fact that the maximum of the evaporating power of the air (the evaporation rate from the porous cup atmometer in this instance) always occurred, in the cases cited, somewhat later in the day than did the maximum of relative transpiration (the ratio of transpiration rate to that of evaporation). This was interpreted to mean that some internal change had taken place in the leaves, which had begun to retard water loss even while the evaporating power of the air had still continued to increase. Such

[1] Botanical contribution from the Johns Hopkins University, No. 22.

postulated change would not necessarily result in a decrease in the actual rate of water loss, thus forming a maximum point in the graph of *absolute* transpiration, but might merely *retard the increase* in this rate and thus give that graph a *lower slope* as it approaches its later-occurring maximum. The graph of *relative* transpiration, however, should show a definite maximum at the point when this retarding change was applied, since this graph is entirely independent of the direct effects of variations in the evaporating power of the air.

The maximum of absolute transpiration might occur at the same time as that of relative transpiration (when the postulated retarding influence may be considered as of greater magnitude than the accelerating influence of the still increasing evaporating power of the air), or it might occur later (when the acceleration due to the increasing evaporation rate may be considered as of greater influence than is the internal retardation). In fig. 8 of the publication to which we are referring, two of these maxima in the graph of absolute transpiration ("Rta") occur simultaneously with maxima in relative transpiration, while another occurs later than that in relative transpiration but earlier than the maximum in the graph of evaporation. The first two cases fulfil the former and the third the latter of the two suppositions made above.

In seeking to examine this daily retardation somewhat more closely, it was found (Publ. 50 still) that the maximum in relative transpiration thus evidenced might occur at almost any hour before the evaporation maximum, but that its occurrence usually fell in the hours between 10:00 A.M. and 1:00 P.M. This maximum, furthermore, appeared to be related to temperature. "As far as the limited data at hand can be trusted, the temperature of the surrounding air seems to be the controlling condition which governs this regulative response. . . . . There is some evidence that intensity of evaporation is the controlling factor, in some cases at least."[2]

From eleven cases on the graphs of the contribution just cited, we have calculated the amount of decrease in relative transpiration

[2] LIVINGSTON, B. E., The relation of desert plants to soil moisture and to evaporation. Publication 50 of the Carnegie Institution, 1906, pp. 63–64.

which was manifest at the time of the evaporation maximum. Thus, at its maximum, the relative transpiration ratio of *Euphorbia* (Publ. 50, Carnegie Inst., fig. 8) is 0.069, this ratio falling rapidly and becoming only 0.035 at the time when the highest evaporation rate for the day is reached. Thus, during the period indicated the retardation of relative transpiration has amounted to 50.8 per cent. On the second day this retardation amounts to 33.3 per cent. The average percentage decrease for the eleven cases is 48.6 per cent, there being little variation in the terms of the series (33.3 is the smallest, the next higher is 41.8, and the largest is 61.2), and we may conclude that the retardation in water loss, for this period, is about 49 per cent. It is improbable that there occurred any closing of stomata during the period involved in this calculation, for the maximum in the evaporating power of the air always occurred long before sunset. Indeed, the retardation which is manifest before any stomatal closing is to be expected is of a considerably higher magnitude than that taken in our calculation, so that the average value of this retardation is surely somewhat greater than that given here.

With this approximation of the magnitude of the internal retardation of water loss, and with the above observation as to its time of occurrence in the day (10:00 to 1:00), we may attempt to ascertain what may be its probable cause.

Preliminary considerations

(1) Incipient drying

In some recent studies[3] bearing upon the quantitative relation between the intensity of sunlight and transpiration, it has been emphasized more than heretofore how important an accelerating influence sunshine may exert upon the rate of water loss from green plants. This influence of solar intensity upon transpiration rate led the writer of the paper last cited to suggest that the internal retardation in water loss which occurs prior to the maximum rate of

[3] Livingston, B. E., (1) Light intensity and transpiration. Bot. Gaz. **52**:417–438. 1911.

———, (2) A radio-atmometer for comparing light intensities. Plant World **4**: 96–99. 1911.

evaporation for the day may be due largely to an increase in the rate of *water loss itself*, as this may be brought about by a rise in the air temperature and especially by absorption of solar energy. This supposition has the appearance of a paradox, since the acceleration of a process is postulated as causing a retardation of the same process, but such phenomena are not infrequent where disturbances in the equilibrium of a system are dealt with, and the suggestion seems worthy of careful theoretical and experimental consideration.

On purely a-priori grounds it is readily understood from the principles of thermodynamics, that a rise in the temperature of the air which bathes the leaves (such as normally progresses throughout the forenoon and well into the afternoon) should produce an ever-increasing vapor pressure of water within the internal atmosphere of the foliar tissues and over the cuticular surfaces. Such an increase in vapor pressure within would usually be adjusted *pari passu* with the rise in temperature, by the ejection of an increasing amount of water vapor through the stomatal openings, and if the temperature were to remain constant for a time the rate of water loss during such a period would be somewhat greater than at the lower temperature, the slightly greater rate being due to the more rapid vaporization and diffusion at higher temperatures.

But the rise in temperature of air and of leaf are not our main consideration with reference to openly exposed green foliage upon a sunny day. Air and leaf do continuously increase in temperature from early morning till some time in the afternoon, but in the meantime the radiant energy of the sunshine is ever being absorbed to a greater or less extent by the green leaf tissue, so that this tissue should tend to become warmer than the air. By far the larger portion of this absorbed energy (a negligible portion disappears through photosynthetic changes) must operate to increase the vapor tension of the water films which surround the foliar air spaces or are held in the epidermal walls. Evaporation from these films must thus be increased, the latter remaining nearly constant in temperature. The accelerated evaporation within the leaf should produce in its turn an increase in the partial gas pressure due to water vapor in the internal atmosphere, and hence, the

stomata being open, a more rapid diffusion, or possibly a molar movement,[4] of water vapor through these openings into the outer air. As long as the sun shines, then, a high rate of transpiration may be maintained, and this without excessively high temperatures in the foliar tissues. The radio-atmometer (LIVINGSTON, see footnote 3) furnishes an excellent example of this kind of effect; with continuous influx of solar energy evaporation from the black porous cup is maintained at a high rate, but the black cup does not exhibit any markedly higher temperature than does the white one, from which water loss is much less rapid.

The Piche atmometer[5] illustrates this process, and also shows another phenomenon which we need to consider here. It consists of a graduated glass tube, closed above and covered below with a circle of filter paper, the latter having a pin hole to admit air to the tube. The tube is filled with water, the paper disk applied and fixed in place, and the whole inverted. The entire disk soon becomes wet, and evaporation therefrom draws water from the tube, air rising through the pin hole to replace the water withdrawn. Now, if such an instrument be arranged with a relatively large disk of paper and placed in conditions of pronounced evaporation, it may often be noted (we are unable to find any mention of this in the literature) that the outer edge of the disk becomes dry, thus vitiating the readings as a measure of the evaporating power of the air. The instrument is unsuited to its purpose unless care be exercised to have the paper so small that the evaporation rate never surpasses the possible rate of outward diffusion to the periphery of the disk. As long as the peripheral portion of the paper remains unsaturated, the actual rate of water loss is maintained nearly constant, the dry area automatically increasing or decreasing in extent according to the fluctuations in the amount of energy

[4] According to the researches and calculations of BROWN and ESCOMBE (Static diffusion of gases, etc., in plants. Phil. Trans. Roy. Soc. London **193**:223–291. 1900), no molar or streaming movement needs to be postulated to explain the highest rates of transpiration observed by these authors in southern Britain. Whether a molar streaming may not occur about midday in the Arizona desert remains an open question.

[5] For literature bearing on this instrument, see LIVINGSTON, GRACE J., An annotated bibliography of evaporation, reprinted from Monthly Weather Review, 1908–1909. The original description is abstracted at page 48 of the reprint under "1872, Piche."

absorbed. Thus, an increase in the evaporating power of the air or in the intensity of impinging solar energy may, with such an instrument, bring about an actual decrease in the extent of the evaporating surface and hence a retardation of water loss. While the actual rate of water loss remains constant so long as the paper is not completely wet, the *relative* rate of water loss (as the loss from the instrument might be compared with that from an open pan of water similarly exposed) begins to decrease as soon as the peripheral portion of the paper begins to dry out. Of course the drying of the disk and the accompanying retardation of relative evaporation are due to a fall below unity of the ratio of possible water supply to water loss; since the rate of possible supply in this instrument remains constant, this means an increase in the denominator of the ratio. A similar result might be occasioned if the rate of loss were to remain constant and the rate of possible supply were to be decreased.

This sort of inadequacy in the rate of water supply to maintain the original evaporating surface during periods of high evaporation may be postulated as perhaps the main feature in bringing about the somewhat sudden fall in relative transpiration observed in the early portion of the day. Indeed, a Piche atmometer may be so arranged, with an abnormally large, preferably *blackened*, disk, so that if compared to a pan of water or to a porous cup atmometer it will exhibit a graph of *relative evaporation* for the daylight hours quite closely paralleling the corresponding graph of relative transpiration for a green plant similarly exposed.

It is only logically conceivable that there exists, for each leaf at any particular time, a maximum possible rate of inward movement of water through the petiole, and if the rate of water loss at any time surpass this possible rate of supply, the tissues of the leaf should become less moist, following the analogy of the Piche atmometer described above. This supposed process of drying out of the foliar cell walls which abut upon the internal atmosphere has been termed *incipient wilting*[6] by the author last cited. It should take place

[6] Since an *incipient* process must be regarded as already actually occurring, it is quite illogical to apply the term *wilting* to a condition of affairs which by definition is not accompanied by any wilting at all. We have therefore adopted the term *incipient drying* in place of the other term.

rapidly at first and more slowly later, the water films gradually retreating into the pores of the cellulose and not only decreasing the extent of the exposed evaporating surfaces, but also greatly increasing the surface tension of the latter. When the surface tension of a liquid film is increased, its vapor tension is correspondingly decreased,[7] so that incipient drying of these exposed cell walls should be accompanied by a marked fall in the rate of vaporization of water therefrom. This should mean nothing less than a measurable retardation in the relative rate of water loss, a retardation *due to an excessive evaporation rate*.[8]

A physical parallel of this phenomenon may readily be arranged by mounting one of two similar paper disks as in the Piche atmometer, so that it will be constantly supplied with water, and its water content will remain constant during the progress of evaporation, while the second disk is similarly mounted on an empty tube, so that its moisture content will fall with water loss. An experiment of this sort, carried out by weighings in the laboratory, showed that a fall in the moisture content of the paper of 6 per cent produced a corresponding decrease in the rate of evaporation of 5 per cent. Similarly, a fall of 17 per cent in water content was accompanied by an evaporation rate 8 per cent lower than when the paper was saturated. The effect becomes more and more pronounced as the paper dries out; when only 54 per cent of the original moisture was present the rate of water loss had diminished to 77 per cent of that from the saturated disk.

[7] PATTEN, H. E., On the relation of surface action to electrochemistry. Trans. Am. Electrochem. Soc. **19**:359–380. 1911. Also, FREUNDLICH, H., Kapillarchemie. Leipzig. 1909. p. 46.

DIXON has presented the only experimental evidence of this with which we are acquainted. DIXON, H. H., Transpiration and the ascent of sap. Prog. Rei. Bot. **3**:1–66. 1909. p. 51.

[8] RENNER has pointed out this same thing: "Denn wenn die Wasserzufuhr ausbleibt, müssen die Membranen trockener werden und damit die Transpiration weiter sinken. . . . ." RENNER, O., Beiträge zur Physik der Transpiration. Flora **100**: 451–547. 1910. p. 516; see also p. 520.

The same author has contributed a most excellent analysis of the water relations of stem and leaf, many points of which have a bearing upon the present question, but we are unable to do more here than merely to mention the paper: RENNER, O., Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**:171–247. 1911.

If the cellulose membranes which are adjacent to the air spaces of the leaf and those bathed by the outer air were structurally similar to the filter paper used in the test just described, the above figures might be applied to the moist foliar surfaces. But we may be sure that filter paper possesses a much less compact structure than any cell membrane in the plant; hence, the reduction in the evaporation rate brought about by partial drying out of the moist cell walls should be much more marked in the case of the latter than is manifest in our experiment. It seems quite probable that a reduction of 50 per cent in the water content of exposed cellulose walls should produce an equal or much greater reduction in the evaporation rate therefrom, and in the case of cutinized epidermis (which holds but little moisture when saturated, and from which cuticular transpiration takes place), the effect of partial drying out should be still greater.

It appears, therefore, quite within the limits of possibility, that the phenomenon of incipient drying of exposed membranes (internal and external) may be adequate to cause the non-stomatal hindrance to transpiration here considered. It should make no difference whether the excessive rate of water loss from foliage leaves be brought about by high evaporating power of the air, by absorption of sunshine, by continually rising temperature, or (merely relatively) by a decrease in the possible rate of water supply (as by the drying of the soil or by the removal or injury of the basal part of the plant), the effect must be the same in every case, namely, a marked fall in the rate of relative transpiration.

If such a process of drying out in leaf tissue were continued, water would eventually be extracted from the protoplasmic membranes, which would in turn remove moisture from the vacuoles, and (since we suppose that the rate of supply from the vascular elements to be inadequate) the turgor pressure would decrease. Finally, all internal pressure would be removed from the cell walls, which would thus cease to be under strain, and all turgidity would thus be destroyed; the wilting point would be reached. Continued still further, the process would result in actual plasmolysis of the cells and finally in death, after which desiccation would rapidly take place. The latter portion of this supposition seems

applicable in all cases when leaves wilt and dry through the influence of too great an intensity of transpiration or too low a maximum possible rate of water supply, these two causes being merely different aspects of the same condition, namely, that the ratio of supply to demand is less than unity.

(2) Other possible factors in the production of an internal resistance to water loss

Logically, there are other possible causes for the observed fall in relative transpiration; it might be regarded as brought about by increased concentration either of the extracellular liquid (in and upon the cell walls), or of the cell sap within the cell vacuoles (as by photosynthesis), or by decreased permeability (perhaps some sort of hardening or coagulation) of the protoplasmic layer itself. The recent work of Fitting[9] shows that the osmotic pressures in the vacuoles of the foliage of desert plants in moist soil (these conditions agree with those of Livingston's plants) are usually isosmotic with a solution less concentrated than 2-molecular potassium nitrate. The fact that no wilting was apparent in the Arizona experiments upon which we are basing our work (which means that turgidity was maintained) indicates clearly that the concentration of the cell sap must have been *higher* than that of the extracellular solutions. Thus the maximum concentration of the evaporating solutions which can be postulated is surely no greater than that of a 2-molecular solution of potassium nitrate, and in order to be certain that our error is in the right direction, we may assume maximum concentrations isosmotic with a 3-molecular solution of this salt. The minimum concentration (as in the early morning) can never be zero, but we once more take this as an assumed limit far beyond the actual, and ask the question, if the foliar solutions vary from pure water to a concentration isosmotic with 3-molecular potassium nitrate, what may be the relative magnitude of the resulting retardation of evaporation? Other conditions being equal, evaporation is known to be proportional to the vapor tension of

[9] Fitting, Hans, Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeitschr. Bot. **3**:209–275. 1911. See also Livingston, B. E., The relation of the osmotic pressure of the cell sap in plants to arid habitats. Plant World **14**:153–164. 1911.

the evaporating surface, and the vapor tension (and hence the evaporation) of a 3-molecular solution of potassium nitrate is only about 8 per cent lower than that of pure water. A comparison of this figure with 49 per cent, the approximated retardation in transpiration, leads us to conclude that an increased concentration and the accompanying lowerings of vapor tension of the foliar solutions cannot possibly be directly related to the great fall in relative transpiration which is observed.[10] That such variations in concentration may have some indirect effect is highly improbable, and there is no evidence at hand to enable us to consider this possibility here. That a slight diurnal increase in the concentration of solutions bathing the protoplasmic membranes might bring about marked changes in the colloidal state of the latter, and hence in their permeability to water, is of course possible; but if such were the case, the effect would be manifest simply as a lowering of the possible rate of supply to the cell walls, resulting in a partial drying out of these, so that the phenomenon would appear as incipient drying.

We conclude, therefore, that the hypothesis of incipient drying, due to partial drying of exposed membranes, is the only adequately possible explanation of the diurnal fall in relative transpiration. If this process actually occurs, it should be exhibited in a sensible decrease in the actual moisture content of the leaves concerned. We should thus expect to find the moisture content of sun-illuminated foliage to become less as the day advances, attaining a minimum some time in the afternoon and then rising again. Whether or not this is actually manifest, as a diurnal fall in the percentage of foliar moisture, is the question which we have experimentally attacked.

It needs to be added here that the hypothesis of incipient drying, while apparently the only logically possible explanation of the non-stomatal *hindrance to water loss*, is not the only logically possible cause of a marked diurnal *fall in the relative water content of* green leaves. With the actual water content of the tissues remain-

[10] This conclusion is quite in accord with that reached by DRABBLE and DRABBLE. See DRABBLE, E., and DRABBLE, H., The relation between the osmotic strength of cell sap in plants and their physical environment. Biochem. Jour. **2**: 117–132. 1907.

ing constant, a diurnal accumulation of non-aqueous materials, as of carbohydrates, oils, proteins, etc., might result in a great increase in the contained non-aqueous material, and a corresponding fall in the percentage of moisture. Such an accumulation, with its accompanying decrease in the percentage of moisture, however, would have no marked influence upon relative transpiration. This question may be studied quantitatively through the daily fluctuations in relative water content on the basis of unit leaf area, a phase of the problem with which we have not concerned ourselves.

Experimentation

Our method of experimentally attacking the problem as to whether a definite diurnal fall in the percentage of leaf moisture actually occurs was to gather, at different hours of the day and night, a large number of similar leaves from plants growing in the open soil, and to determine the percentage of moisture therein contained by the common method of weighing, drying at 100° to 105° C., and reweighing. As the leaves were gathered they were placed immediately in tarred glass bottles and tightly stoppered. After being weighed, the open bottles were placed in the drying oven, and the final dry weight obtained without removing or handling the leaves. A large number of plants were available for this work, so that but few leaves were taken from the same plant, and the numerical result may be taken as fairly well approximating the average condition of the whole plot of plants of the species tested. The plants used were all spontaneous in the open ground near the Desert Laboratory. In some cases the sample leaves were taken every two hours, in others less often, and a porous cup atmometer was operated and read at short intervals in the vicinity of the group of plants from which leaves were taken. The work was carried out at the Desert Laboratory of the Carnegie Institution at Tucson, Arizona, in the summer of 1910.

Preliminary tests of the leaf moisture in *Physalis angulata* var. *Linkiana* Gray and in *Martynia louisiana* Mill., made on July 28, showed that the moisture content of the *Physalis* leaves was 744.7 per cent of the dry weight at 6 A.M., and only 561.0 per cent at 2 P.M., while the corresponding percentages in *Martynia* leaves were

543.3 and 377.3 per cent, respectively. Expressed in another way, the non-aqueous materials of the leaves made up for *Physalis* 12 per cent of the whole in the morning and 15 per cent in the afternoon, while for *Martynia* these quantities were 16 and 21 per cent, respectively. It thus became clear that there had occurred a marked fall in the relative moisture content of these leaves during the period from 6 A.M. to 2 P.M., which is what our a-priori considerations had led us to expect, and our problem seemed to be answered in the affirmative.

We present, in the four following tables, the data derived from a number of other tests, carried out by a method quite similar to that followed in the two tests just described. Besides the two plants named above, we dealt with *Nicotiana glauca* Graham (a woody perennial attaining the proportions of a tree), *Euphorbia heterophylla* L., *Trianthema Portulacastrum* L. (a fleshy plant resembling *Portulaca oleracea* L. of the east), *Tribulus terrestris* L., *Sida angustifolia* Lam., *Amarantus Palmeri* Wats., *Maclura pomifera* (Raf.) Schneider, *Covillea glutinosa*, and *Prosopis velutina* Wooton. The two last-named plants are characterized by thin, hard, xerophyllous leaves, the foliage of *Covillea* (the creosote bush) being heavily covered with a shellac-like resinous layer. For the naming of our experimental plants we are indebted to the kindness of Professor J. J. THORNBER, of the University of Arizona.

Tables I to IV present the evaporation rates for the periods in question, in terms of cc. from the standard porous cup atmometer.[11] The moisture contents of the leaves are given in percentages of their dry weight, also the dry weights in percentages of total weight. In the first two columns appear periods and evaporation rates per hour (cc.) from the porous cup atmometer, these data being quite comparable throughout all four series. Evaporation maxima are designated by asterisks. In the third column are presented the hour at which leaf tests were made. The remainder of each table presents the leaf moisture data, each minimum being denoted by an asterisk in the second column for each plant, and all the maxima by full-faced type.

[11] LIVINGSTON, B. E., Operation of the porous cup atmometer. Plant World 13:111–118. 1910.

It is at once apparent that in all cases but three (nine out of eleven species) our question (page 319) has been answered very definitely in the affirmative.[12] In the case of *Prosopis* (table III) the minimum water content, at midday, is only slightly below that in

TABLE I

AUGUST 12–13, 1910

EVAPORATION		PERCENTAGE OF MOISTURE							
			Martynia		Sida		Amarantus		
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)								
6– 7	0.66	6	417.6	81	452.8	82	539.4	84
7– 8	1.14	7	390.0	80	**484.3**	**83**	533.3	84
8– 9	2.28	8	394.6	80	412.5	80	551.2	85
9–10	2.34	10	384.2	79	353.7	78	500.7	83
10–11	2.58	..	.....	..	.....	..	.....	..
11–12	2.52	12	357.6	78	355.7	78	490.6	83
(P.M.)								
12– 1	3.48	..	.....	..	.....	..	.....	..
1– 2	3.90	2	339.3	77	338.9	77	395.0	80
2– 3	3.54	..	.....	..	.....	..	.....	..
3– 4	3.72	4	338.4	77*	307.3	75*	379.6	79
4– 5	4.02*	..	.....	..	.....	..	.....	..
5– 6	2.52	6	371.2	79	317.1	76	366.6	79*
6– 7	1.56	..	.....	..	.....	..	.....	..
7– 8	1.44	8	**551.6**	**85**	407.2	80	591.5	86
8– 9	1.32	..	.....	..	.....	..	.....	..
9–10	1.08	10	502.7	83	444.4	82	539.2	84
10–12	0.69	12	461.5	82	457.1	82	**601.9**	**86**
(A.M.)								
12– 4	0.125	4	494.7	83	457.0	82	530.0	84
4– 5	0.72	..	.....	..	.....	..	.....	..
5– 6	0.60	6	455.1	82	.....	..	542.1	84

the early morning, and the maximum, at 4 P.M.. is not markedly above the minimum; this case is questionable. One of the two definite exceptions to the general rule, *Covillea* (table III), appears to exhibit a reversal of the usual variation in water content. The fact that this plant and *Prosopis* are non-succulent xerophytes is

[12] At about the same time that our experiments were in progress, LLOYD carried out his recently published tests in regard to this same matter in *Fouquieria*. He finds and discusses a diurnal fall in the relative water content of the foliage of this plant. LLOYD, F. E., The relation of transpiration and stomatal movements to the water content of the leaves in *Fouquieria splendens*. Plant World **15**:1–14. 1912.

possibly to be correlated with their peculiar behavior, and it may be suggested that such permanent structural retardation of water loss as is present in the foliage of such types may have to do with preventing a marked decline in leaf moisture by day. Such plants seem worthy of further study in this connection. The other excep-

TABLE II

AUGUST 21–22, 1910

EVAPORATION		PERCENTAGE OF MOISTURE											
			Physalis		Nicotiana		Euphorbia		Trianthema		Tribulus		
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	
(A.M.)													
4– 5	0.06	5	.....	..	**588.7**	**85**	.....	..	.....	..	**435.6**	**81**	
5– 6	0.06	..	.....	..	.....	..	.....	..	.....	..	.....	..	
6– 7	0.50	7	820.2	89	.....	..	**581.6**	**85**	**1203.9**	**92**	.....	..	
7– 8	1.20	..	.....	..	.....	..	.....	..	.....	..	.....	..	
8– 9	1.92	9	865.5	90	435.0	81	521.6	84	1197.9	92	352.5	78*	
9–10	2.10	10	804.6	89	.....	..	.....	..	.....	..	.....	..	
10–11	2.40	11	818.9	88	.....	..	.....	..	.....	..	.....	..	
11–12	2.58	..	.....	..	.....	..	.....	..	.....	..	.....	..	
(P.M.)													
12– 1	2.40	1	678.5	87	423.3	81	433.8	81*	758.0	89*	378.8	79	
1– 2	2.88	..	.....	..	.....	..	.....	..	.....	..	.....	..	
2– 3	2.94*	3	660.6	87*	.....	..	.....	..	.....	..	.....	..	
3– 4	2.70	..	.....	..	.....	..	.....	..	.....	..	.....	..	
4– 5	2.70	5	703.4	87	392.5	80*	485.5	83	825.2	89	420.1	81	
5– 6	1.92	..	.....	..	.....	..	.....	..	.....	..	.....	..	
6– 7	1.20	7	**877.9**	**90**	.....	..	.....	..	.....	..	.....	..	
7– 8	1.20	..	.....	..	.....	..	.....	..	.....	..	.....	..	
8– 9	1.20	9	855.7	90	.....	..	480.9	83	.....	..	430.6	81	
9–10	0.90	..	.....	..	.....	..	.....	..	.....	..	.....	..	
10–11	1.98	..	.....	..	.....	..	.....	..	.....	..	.....	..	
11–12	1.14	..	.....	..	.....	..	.....	..	.....	..	.....	..	
(A.M.)													
12– 1	0.42	..	.....	..	.....	..	.....	..	.....	..	.....	..	
1– 2	0.42	..	.....	..	.....	..	.....	..	.....	..	.....	..	
2– 3	0.18	3	848.2	89	.....	..	.....	..	.....	..	.....	..	

tion to the usual behavior is that of *Physalis* (table IV). For this species we have two cases exhibiting the usual behavior (besides the preliminary test, which makes three), and it is noted that the exceptional case occurs on a day with very low evaporation.

Table V presents a summary of the data of the preceding tables. The minimum and maximum water content and the hours at which

these occurred, the latter being simply numbered from 1 to 24, are there given, together with the corresponding maximum rate of evaporation and the hour of its occurrence.

TABLE III

AUGUST 28–29, 1910

EVAPORATION		PERCENTAGE OF MOISTURE									
			Physalis		Maclura		Covillea		Prosopis	
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)										
6– 7	0.82	7	778.5	89	**237.2**	**70**	116.7	54*	159.7	61
7– 8	2.37	..	.....	..	.....	..	.....	..	.....	..
8– 9	2.87	9	736.7	88	224.1	69	127.4	56	145.3	59
9–10	3.77	..	.....	..	.....	..	.....	..	.....	..
10–11	4.51	11	595.2	86	.....	..	.....	..	.....	..
11–12	4.92	..	.....	..	.....	..	.....	..	.....	..
(P.M.)										
12– 1	5.08*	1	566.2	85*	186.6	65	125.1	56	144.3	59*
1– 2	4.67	..	.....	..	.....	..	.....	..	.....	..
2– 3	3.03	3	625.9	86	173.8	63*	.....	..	.....	..
3– 4	3.69	4	.....	..	.....	..	**139.3**	**58**	**168.4**	**61**
4– 5	2.13	5	780.6	89	.....	..	.....	..	.....	..
5– 6	1.56	..	.....	..	.....	..	.....	..	.....	..
6– 7	1.15	7	**781.1**	**89**	.....	..	.....	..	.....	..
7– 8	1.56	..	.....	..	.....	..	.....	..	.....	..
8– 9	0.90	9	772.1	89	186.9	65	.....	..	.....	..
9–10	0.90	..	.....	..	.....	..	.....	..	.....	..
10–11	0.57	11	761.5	88	.....	..	.....	..	.....	..
11–12	0.49	..	.....	..	.....	..	.....	..	.....	..
(A.M.)										
12– 1	0.74	1	696.1	87	.....	..	.....	..	.....	..
1– 2	0.33	..	.....	..	.....	..	.....	..	.....	..
2– 3	0.41	3	705.4	88	.....	..	.....	..	.....	..
3– 4	0.33	..	.....	..	.....	..	.....	..	.....	..
4– 5	0.33	5	743.4	88	.....	..	.....	..	.....	..
5– 6	0.82	..	.....	..	.....	..	.....	..	.....	..
6– 7	1.48	7	755.2	88	.....	..	.....	..	.....	..

Physalis is the only form which was tested on different days, with different conditions of evaporation, and the data therefrom are the most instructive of our series. In the first two cases this form showed the greater variation in water content with the higher evaporation maximum (5.08 cc. per hour, table III), and the smaller variation with the lower evaporation maximum

(2.94 cc. per hour, table II). In the third test the water variation was slightly (probably within the limits of experimental error) in the opposite direction, as has been noted. The evaporation maximum on this day was relatively low, 2.52 cc per hour (table IV). These relations make it appear that the amount of variation in foliar moisture is directly related to the evaporating power of the air, especially to the maximum intensity of this factor for the day

TABLE IV

AUGUST 30, 1910

EVAPORATION		PERCENTAGE OF MOISTURE		
			Physalis angulata	
Period	cc. per hour	Hour of test	On basis of dry substance	On basis of entire weight
(A.M.)				
7– 8	1.97	7	668.2	87
8– 9	1.56	9	695.0	87
9–10	1.72	..	.....	..
10–11	2.46	11	680.7	87
11–12	2.30	..	.....	..
(P.M.)				
12– 1	2.30	1	**714.7**	**88**
1– 2	2.52*	..	.....	..
2– 3	2.30	3	662.3	87*
3– 4	2.30	..	.....	..
....	....	..	.....	..
4:30–5:30	0.97	5:30	665.7	87

NOTE.—The day was almost wholly cloudy, which accounts for the generally low evaporation rates and the small fluctuations.

in question. With great evaporation there appears to be a great diurnal fall in moisture content, with less evaporation a less pronounced fall, and with still less evaporation no fall at all, possibly even a slight rise.

Only a single test, with measurement of evaporation, was carried out with each of the remaining forms. The greatest variations were exhibited by *Martynia*, *Amarantus*, and *Sida*, all of them being plants which have been repeatedly observed to wilt very readily under drought conditions. The only true succulent tested was *Trianthema*, which showed a variation markedly greater than that of *Physalis* for the same day (table II). *Nicotiana* and

Euphorbia gave variations equaling *Physalis* (tables II and III); those of *Tribulus* and *Maclura* were markedly less; while, as already noted, *Prosopis* and *Covillea* evidence very small variations, that of the latter rather definitely in the opposite direction.

Scrutiny of table V brings out the fact that the hours of minimum relative water content for the prevailing type of leaves falls generally within an hour or two of that of the maximum evapora-

TABLE V

SUMMARY OF TABLES I–IV

PLANT	MINIMUM MOISTURE CONTENT		MAXIMUM MOISTURE CONTENT		MAXIMUM OF EVAPORATION	
	Percentage	Hour	Percentage	Hour	cc.	Hour
Martynia (table I)..	77	14	85	20	4.02	16–17
Sida (table I).....	75	16	83	7	4.02	16–17
Amarantus (table I)	79	16, 18	86	20, 24	4.02	16–17
Physalis (1) (table II)	87	13, 16	90	19, 21	2.94	14–15
Physalis (2) (table III).....	85	13	89	17, 19, 21	5.08	12–13
Physalis (3) (table IV).....	87	15, 17½	88	13	2.52	13–14
Nicotiana (table II)	80	17	85	5	2.94	14–15
Euphorbia (table II)	81	13	85	7	2.94	14–15
Trianthema (table II).....	89	13, 17	92	7, 9	2.94	14–15
Tribulus (table II)..	78	9	81	5, 17, 21	2.94	14–15
Maclura (table III).	63	15	70	7	5.08	12–13
Covillea (table III).	54	7	58	16	5.08	12–13
Prosopis (table III).	59	9, 13	61	7, 16	5.08	12–13

tion rate. The minimum moisture content occurs between 1:00 P.M. and 5:00 P.M. for all cases except those already noted as exceptional, and that of *Tribulus* (table II), which has its minimum at 9:00 A.M.

The evidence from *Physalis*, indicating clearly a definite relation between the magnitude of the moisture variation and the intensity of evaporation, may be interpreted to mean that the variation is due primarily to incipient drying (to a removal of water by transpiration more rapidly than its entrance into the leaves), and not to an accumulation of non-aqueous bodies in the leaf cells. It seems extremely improbable that a diurnal accumulation of plastic materials should exhibit such a parallelism with the evaporation

as do our data of moisture variation, from which consideration it may be concluded that the variation is probably not causally related to such accumulation of substances. While there are several observations in the literature which bear more or less directly upon this matter of the diurnal accumulation of soluble and insoluble bodies in the leaf, we do not as yet possess data adequate to a logical discussion. This should be made the subject of a special study in the present connection.

Following the criterion of the *time of occurrence* of the minimum water content (2 to 5 P.M.) and of that of the maximum in relative transpiration, as brought out in Publ. 50, Carnegie Inst. (10 A.M. to 1 P.M.), it appears highly probable that there exists a causal relation between these two phenomena. Since the critical point in the graph of relative transpiration denotes, as has been pointed out, the entrance into operation of some internal check or hindrance to the loss of water vapor, and since a decrease in relative water content should be effective to produce such a check long before the water content had attained its minimum, we should expect the maximum in relative transpiration to occur long before the hour of least foliar moisture, which it appears actually to do. We may conclude tentatively, and on general lines, that, for the ordinary types of leaves, the retardation in water loss is manifest several hours before the time of minimum water content. After the critical point in relative transpiration, the non-stomatal retardation of water loss appears to be (Publ. 50) continuously active until well into the night, its effects becoming mingled with those of stomatal closure at or about sunset. It appears to be gradually removed during evening and early night, so that in the hours just preceding sunrise stomatal retardation seems to be alone manifest. If the non-stomatal effect be due to decreased water content, it should be removed when the leaves had regained their normal moisture, which condition is quite met by the observations. The maximum in moisture content (except in the few erratic cases already mentioned) occurs in the night or early morning, just as our hypothesis demands.

The only direct comparison between the daily march of leaf moisture and that of relative transpiration which has been made

thus far, was carried out on August 21 and 22. From 5 A.M. on the first day till 6 A.M. on the second, hourly weighings were made on two potted and sealed plants of *Physalis*, while corresponding readings were obtained from a porous cup atmometer having the same exposure. The two plants were similar to each other and, though somewhat smaller, not dissimilar to the *Physalis* plants of the leaf moisture tests of the same period (table II), so that the two series of data are fairly comparable. Space will not permit the presentation here of the transpiration and evaporation rates and of the resulting ratios and graphs, but we may mention the findings of most present interest. Averaging the data for the two plants (these data are very similar), the maximum of absolute transpiration occurred from 11 A.M. to 12 noon, while the maximum rate of loss from the porous cup atmometer fell three hours later. The maximum of relative transpiration occurred from 12 noon to 1 P.M.; thus the non-stomatal retardation of water loss became effective about 1 P.M. As already shown (table II), the moisture content of the leaves of *Physalis* in the open soil fell during the period from 9 A.M to 3 P.M., and rose again to its maximum, or what we may term its normal, at 7 P.M. From these data we see that the non-stomatal retardation of water loss became manifest in the potted plants four hours after the leaf moisture had begun to decrease in the plants in the open, and two hours before the occurrence of the minimum water content. The maximum evaporation rate occurred in the hour preceding the minimum water content. All of these points are quite in harmony with the requirements of the hypothesis of incipient drying, and the data appear to substantiate this hypothesis, so far as their incomplete nature will allow.

The work of BRIGGS and SHANTZ[13] on some of the conditions which determine wilting has thrown not a little indirect light upon the question of the occurrence of incipient drying. By the ingenious balanced system which these authors devised, they have shown clearly that, with the gradual drying out of the soil, there comes a time when the rate of entrance of water into the upper part of a plant is surpassed by the transpiration rate. This is, of course,

[13] BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient for different plants and its indirect determination. Bur. Pl. Ind. Bull. 230. 1912.

the condition of incipient drying. Judging from the rates of transpiration shown by the tables of this contribution (no attempt is made to define the aerial conditions), it appears that the evaporating power of the air during the experiments there described was relatively low. This fact rendered the process of incipient drying, which leads eventually to actual wilting, very much prolonged, and it is perhaps not surprising that these authors failed to detect incipient drying in the plants which actually wilted, making the mistake of supposing that incipient drying in the non-wilting forms (as cactus, lemon, etc.) is to be considered as identical with actual wilting (which is relatively a much later occurrence) of ordinary thin-leaved plants. It is greatly to be regretted that such an expensive and elaborate series of determinations as BRIGGS and SHANTZ have made should have been carried out without records of the intensity and duration aspects of the evaporating power of the air under which the experiments were performed. Such records, which are perhaps the most readily obtained of all the climatic records which are as yet available for the study of plant processes, would have made possible the duplication of the aerial conditions of these experiments and would have aided greatly in the further analysis of some of the important findings of these authors.

Conclusions

We conclude from our measurements and comparisons that there can remain little question that green plants when subjected to relatively great diurnal evaporation intensity, at least frequently exhibit a marked fall in foliar moisture content by day and a corresponding rise by night. The daily march of evaporation remains still to be studied in other climates than that of summer in southern Arizona, so that we are unable to compare our conditions with those of more humid or cooler regions. From our experience with cloudy weather, we are inclined to the prediction that the diurnal decrease in leaf moisture here established for high evaporation rates may fail to occur in regions of low evaporation when accompanied by relatively high rates of soil moisture supply.

Our studies also indicate that some non-succulent, small-leaved xerophytes (such as *Covillea* and *Prosopis*) fail more or less com-

pletely to exhibit a diurnal fall in foliar moisture under conditions of evaporation which render it manifest in the common type of thin-leaved plants (such as *Martynia*, *Sida*, *Physalis*), as well as in such pronounced succulents as the *Portulaca*-like *Trianthemum* of our work. It is suggested that these exceptional small-leaved xerophytes may actually show a somewhat higher leaf moisture content by day than by night, but this proposition is uncertain.

While the other logically possible cause of this diurnal decrease in relative water content of foliage leaves, namely, a diurnal increase in materials other than water within the tissues, remains still to be considered in a thoroughly adequate way, our findings fail to adduce evidence in favor of this as the true cause of the observed phenomena, and do furnish several lines of indirect opposing evidence. It may be stated, therefore, that, so far as evidence is at hand (including indirect considerations of the literature, not here cited), it is probable that the cause of this diurnal minimum in foliar moisture rests in the phenomenon of incipient drying, brought about whenever the ratio of water loss to water supply in the leaves is rendered less than unity. It may thus be suggested that, although our tests with *Physalis* would lead to the conclusion that the external factor which controls this diurnal fall of leaf moisture is evaporation intensity simply, the true controlling condition is more probably the ratio of water supply to water loss. Thus, the structure of the plant (including all of its various "adaptations" to dry habitats), the moisture conditions of the soil, intensity of evaporation and of solar illumination appear to make up the controlling environmental complex.

It seems highly probable from our studies that the diurnal, non-stomatal retardation of the escape of water vapor from green leaves in sunlight (as first described in Publ. 50, Carnegie Inst., and there attributed to the influence of temperature or evaporation intensity) is but the effect of a lower vapor tension within the internal atmosphere of the leaves and over their surfaces, this lower vapor tension being brought about by the increased surface tension and decreased evaporating surface which accompanies a lowered water content of the internally and externally exposed cell walls.

In conclusion, it may be suggested that we have here, in the

diurnal minimum in the water content of foliage leaves, a criterion that may be of some importance to scientific agriculture, at least in the arid regions of the globe. By this criterion it may be possible to determine indirectly, and somewhat simply, the status of the water relations of the plant, and indeed to foresee the need of increased soil moisture, long before the usual criterion of cessation of growth or actual wilting becomes manifest.

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RAY TRACHEIDS IN ABIES

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(WITH PLATES XXIV AND XXV)

A characteristic feature of the Abietineae, as opposed to the remaining tribes of the Coniferales, is the possession of ray tracheids in their wood. To this statement exception must be made, on the one hand for the genera *Abies* and *Pseudolarix*, from which they have hitherto been regarded as quite absent, and on the other hand for a few species of the Taxodineae and Cupressineae, in which they have been reported to occur sporadically. Even in the latter, however, they never become normal features as in the Abietineae. This distribution has recently received two interpretations. PENHALLOW[1] held that in the species where they occur sporadically they are appearing for the first time, and from this condition develop to their culmination in the Abietineae. JEFFREY,[2] on the other hand, having observed their occurrence in association with a wound in *Cunninghamia sinensis*, regards their sporadic appearance as a reminiscence of an original abundant condition such as exists in the Abietineae. The application of these conflicting views in phylogenetic considerations of the whole family is obvious.

To the distribution briefly outlined above, the writer[3] recently recorded an exception in the case of the genus *Abies*. In a wounded root of *A. amabilis* ray tracheids were discovered in considerable numbers. The only other record of their occurrence in the genus was made by PENHALLOW (*loc. cit.*), who observed them sporadically in *A. balsamea*. In view of the peculiar circumstances of their discovery and its bearing on the theories in vogue, it was considered advisable to investigate the material of *A. amabilis* fully and to examine other species of the genus.

The material in which the marginal tracheids were observed

[1] PENHALLOW, D. P., North American Gymnosperms. Boston. 1907.

[2] JEFFREY, E. C., Traumatic ray tracheids in *Cunninghamia sinensis*. Ann. Botany **22**:602. *pl. 31*. 1908.

[3] THOMPSON, W. P., The origin of the ray tracheids in the Coniferae. BOT. GAZ. **50**:101–116. 1910.

consisted of a segment of a root several inches in length and containing about 25 annual rings. On one side a severe wound had been partially healed over. A photograph of a transverse section taken some distance above the wound is presented in fig. 1. Even at this low magnification, characteristic tangential series of traumatic resin canals may be observed in the 5th, 6th, 9th, and 12th annual rings. Therefore, the root must have been wounded at least four times. The repeated wounding had apparently sapped its vitality, for the later-formed annual rings were very narrow and infested with fungus filaments.

A more magnified view of one of the series of canals is shown in fig. 2. The arrangement is seen to be typically traumatic. In other respects the wood is of the normal *Abies* type.

A radial longitudinal section, taken at some distance from the outermost wound, is photographed at rather low magnification in fig. 3. Near the left of the figure the septated element and its neighbor on the right, which is also septated beyond the limits of the figure, form part of the traumatic series between the canals. Immediately on their right two ray tracheids are to be seen on the upper margin of the ray. The magnification is not sufficient to show the character of their pits except that they are smaller than those of neighboring wood tracheids.

The character of the pits on a similar element may be distinguished, however, in fig. 4, which is a photograph at a higher magnification of another section. Two of the pits in section on the extreme left are clearly bordered on the upper side and simple on the parenchyma side. The others, though not so clear, are likewise unilaterally bordered; therefore the long low element is a ray tracheid.

That interspersed as well as marginal tracheids are present is shown in fig. 5. The two pits on the conspicuous vertical end wall are distinctly bordered, as are those on the horizontal walls of the same cells. Therefore, these cells are ray tracheids occurring between the parenchymatous cells of the ray which are to be seen above and below. The parenchymatous cell below the ray tracheid is traversed by a filament of the fungus which probably gained entrance at the wounds.

Elongated ray tracheids of the type described by the writer (*loc. cit.*) as common in the young root of *Pinus* were also frequently observed. One of them is shown in fig. 9. The tail-like projection extends to the extreme upper right of the figure. A unilateral bordered pit may be observed in contact with the ray and a bilateral one in contact with a wood tracheid.

The figures just described show that ray tracheids of all kinds are present in this wounded root of *A. amabilis*. Normal material of the same species, root, stem, and branch was carefully examined, and, in accordance with all former observations, not a single ray tracheid found. Therefore, it must be concluded that those observed were in definite association with the wounds. In fact, their occurrence recalls precisely that described by JEFFREY for *C. sinensis*. Occurring, as they do, in one of the two abietineous genera which normally are entirely without them, their presence is all the more significant.

In JEFFREY'S material of *Cunninghamia* the ray tracheids were found only on the side remote from the wound. In my material this was not the case, as they were often in direct contact with the traumatic canals. Of course, the position of the various traumatic series (see fig. 1) would indicate that the root had probably been wounded at different points on its circumference, and therefore even if JEFFREY'S observation held good for this material, the ray tracheids ought to be found on any radius. However, in material of another species to be described immediately, such was distinctly not the case.

Let us now turn to the other species examined. A radial section of a wounded branch of *A. concolor* is shown in fig. 7. The short septated elements at the central part of the extreme left are part of the traumatic series. Following these on the margins of both rays are bordered-pitted elements which are obviously ray tracheids. The conditions existing in the wounded root of *A. amabilis* are thus exactly duplicated in the wounded branch of *A. concolor*. In both species the ray tracheids are often in line with parenchyma cells, as in fig. 7. The usual condition is the appearance of one or two parenchymatous cells in the summer wood and a similar number of ray tracheids conterminous with them in the first-formed spring

wood of the following year. Between these and the summer wood of the same year neither kind of element is to be found.

Another species in which ray tracheids were found is *A. homolepis*. Fig. 8 shows a ray in the region of the annual ring. On the upper margin are ray tracheids in line with a parenchyma cell. Fig. 12 is a more magnified view of these elements, and shows the bordered character of the pits more distinctly, especially of the two on the end wall. The material of *A. homolepis* is particularly interesting from the fact that it exhibited no trace of wounding either in radial or transverse sections. As the segment was of considerable length and contained ray tracheids throughout, the presence of the latter could scarcely have been the result of a distant wound, especially as there was no trace of traumatic canals. Their presence, therefore, must be considered as normal, or at least sporadic.

The only other species in which these structures were observed is *A. Veitchii*. Fig. 11 demonstrates their presence in this form, the bordered pit on the end wall being most distinct. The material was similar to that of *A. homolepis*, a branch which showed no trace of wounding. As in the other species, their typical position was in the spring wood following one or two parenchymatous cells in the summer wood of the previous year (see fig. 11).

Many other species were examined, including *A. lasiocarpa*, *Fraseri*, *Nordmanni*, *cephalonica*, *grandis*, *balsamea*, and *firma*, but none were found to have ray tracheids. A very diligent search was made in the case of *A. balsamea*, in which PENHALLOW reports having observed them sporadically. Normal and wounded roots, stems, branches, and seedlings, as well as witches' brooms, all failed to show a single indisputable ray tracheid. However, material collected during the active growing season and examined in the cambial region showed a slight border on the pits of some of the cells, which from their position were evidently doomed to degeneration in a manner to be described below.

In all those species in which ray tracheids were found, their position and association with neighboring cells were very suggestive. As has been described, they usually occurred in the spring wood, and were conterminous with one to several parenchyma

cells in the summer wood of the previous year (figs. 7, 8, 11). These groups of parenchyma cells at the boundary of the annual ring are characteristic features of many species of *Abies*. In the spring wood they disappear, to be revived again in the following summer wood. The result is the appearance of single cells or small groups of cells scattered along the margins of the rays, each group at the end of an annual ring. Between the groups there is usually no trace of cells, but here and there peculiar "ghostlike" appearances resembling cells may be seen. One of them is shown in fig. 6, which is a photograph of a section of *A. homolepis*. They are shadowy, structureless affairs, staining best in hematoxylon and giving no response to the phloroglucin test for lignin. Occasionally they form an almost continuous cell-like series from one group of parenchyma cells to the next, but usually they are rather isolated. That these structures are not merely thin sections of the sides of actual living cells is shown by their staining qualities, by their lack of structure, and by a study of a series of sections. The only explanation for their presence is that they are degenerated cells. In fact, it is possible to observe, especially in the cambial region, all stages in degeneration from such a conspicuous object as that seen in fig. 6, to ones which are barely discernible even with the strongest staining. The scattered condition is obviously due to the complete disappearance of some members of the series.

Now when ray tracheids occur, they identify themselves definitely with these series of degenerating cells. They may often be observed conterminous with one of the "ghosts." The inference seems irresistible that these "ghosts" were originally complete rows of ray tracheids which have degenerated in most species, but may survive sporadically in a few, and may be recalled traumatically in others.

The groups of parenchyma cells at the end of the annual ring are likewise definitely identified with these degenerating cells, whether ray tracheids are present or not. It seems probable that at the end of the year's growth, when there is a great demand for storage in preparation for the approaching winter, the cells which would otherwise degenerate are given a new lease of life and transformed into parenchyma cells which are capable of storage. That

the transformation has actually taken place is proven by the discovery of intermediate forms of cells. In fig. 10, which is a more magnified view of the lower part of fig. 8, is an element with a distinct bordered pit on its vertical wall and several equally distinct simple pits on its horizontal wall. This element, therefore, is neither a tracheid nor parenchyma cell, but combines the pitting of both. Several such cells were seen, in some cases both kinds of pits occurring on the same wall. So far as the writer is aware, the anomaly of bordered and simple pits occurring on the same element has never been observed except in this laboratory by Miss GORDON[4] in material of *Sequoia*.

A much commoner type of transitional element than the anomalous structures just described is illustrated in fig. 13, from *A. Veitchii*. The pits on the ray tracheid are so slightly bordered as to be scarcely distinguishable from the simple pits of the parenchymatous cells. The figure illustrates but one or two of the many forms intermediate between typically simple and typically bordered pits which may be observed on these elements.

Conclusions

The presence of ray tracheids as a result of wounding in *A. amabilis* and *A. concolor* parallels exactly the phenomena described by JEFFREY for *C. sinensis*. The interpretation advanced by him is that we have here a case of the revival by wounding of structures ancestrally present and lost in the course of evolution. Owing to the closer affinity of *Abies* with those genera in which ray tracheids are abundant, his reasoning applies with even greater force to the observations described in this paper. Again, their sporadic occurrence in uninjured material of a few species of the genus strongly supports this view. Further support is added by the association of the ray tracheids with the degenerating cells or "ghosts," and with the groups of marginal parenchyma cells at the ends of the annual rings. It may be concluded that ray tracheids were present in the ancestors of *Abies*, and have per-

[4] GORDON, MARJORIE, Ray tracheids in *Sequoia sempervirens*. New Phytol. 11:1–7. *figs.* 7. 1912.

sisted sporadically in a few species, but in the majority have either degenerated or been transformed to parenchyma.

Summary

1. Ray tracheids, marginal, interspersed, and elongated, were observed in association with wounds in *A. amabilis* and *A. concolor*.

2. They were also observed in uninjured material of *A. homolepis* and *A. Veitchii*.

3. Their usual position was in contact with a series of degenerated cells on one hand and a group of parenchyma on the other.

4. Transitions from ray tracheids to parenchyma were common, some elements having both bordered and simple pits, and others pits with borders of various sizes.

5. All the evidence points to ray tracheids being present in the ancestors of *Abies* and absent today by reduction.

The writer is indebted to Professor C. S. SARGENT for permission to collect material in the Arnold Arboretum, and to Mr. R. B. THOMSON for material and advice. The work was carried on under appointment as an "1851 London Exhibition Science Research Scholar" of the University of Toronto.

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EXPLANATION OF PLATES XXIV AND XXV

PLATE XXIV

FIG. 1.—*Abies amabilis:* transverse section of wounded root, showing several series of traumatic resin canals; ×12.

FIG. 2.—The same: higher magnification, showing a row of traumatic resin canals; ×100.

FIG. 3.—The same: radial section; ×150.

FIG. 4.—The same: radial section, showing marginal ray tracheid with bordered pits in section; ×800.

FIG. 5.—The same: interspersed ray tracheid; ×1200.

FIG. 6.—*Abies homolepis:* radial section, illustrating the presence of "ghostlike" degenerated cell; ×400.

PLATE XXV

FIG. 7.—*Abies concolor:* radial section, showing wound tissue on the left and ray tracheids on the margin of both rays; ×500.

FIG. 8.—*Abies homolepis;* showing marginal ray tracheids; ×600.

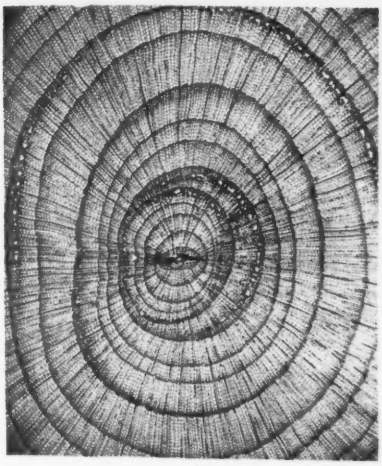
FIG. 9.—*Abies amabilis:* showing vertically elongated ray tracheid; ×800.

FIG. 10.—*Abies homolepis:* showing element with both bordered and simple pits; ×800.

FIG. 11.—*Abies Veitchii:* showing presence of ray tracheid conterminous with parenchyma cell; ×600.

FIG. 12.—*Abies homolepis:* high power to show ray tracheid; ×1000.

FIG. 13.—*Abies Veitchii:* an element with pits very slightly bordered; ×600.



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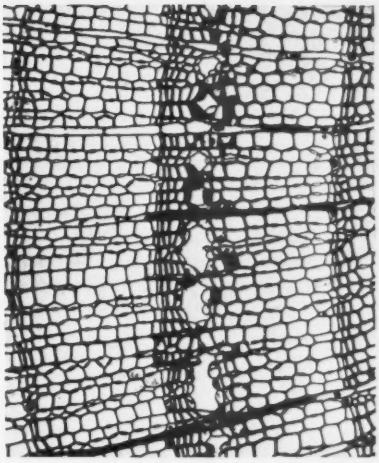

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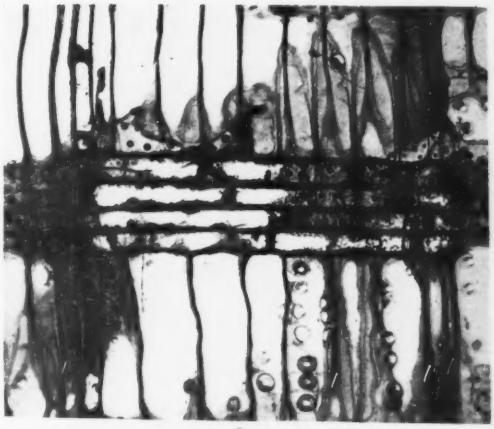

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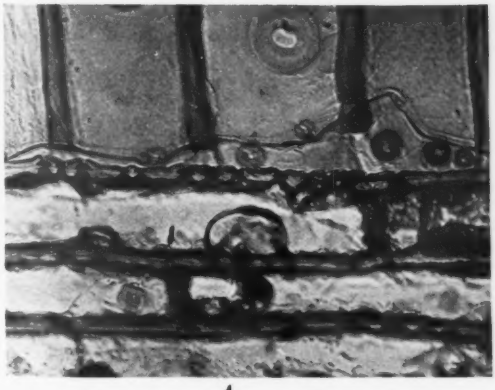

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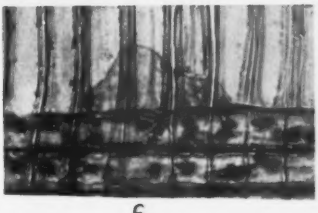

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THOMPSON on RAY TRACHEIDS

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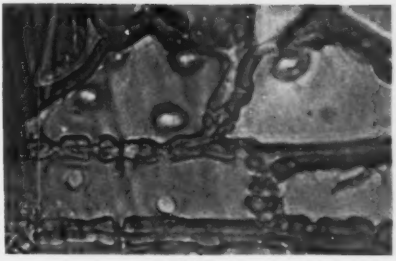

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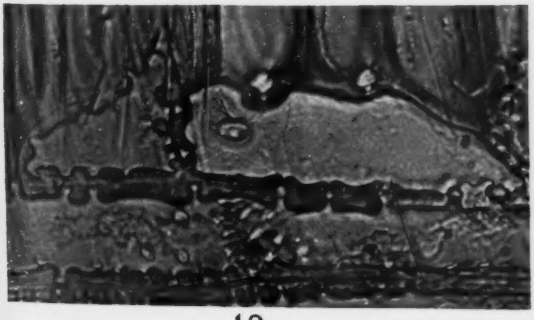

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THOMPSON on RAY TRACHEIDS

DO THE ABIETINEAE EXTEND TO THE CARBONIFEROUS?

ROBERT BOYD THOMSON AND ARTHUR EVERETT ALLIN

(WITH PLATE XXVI AND TWO FIGURES)

JEFFREY and CHRYSLER, in a recent monograph on the Pityoxyla of the Cretaceous (**4**), assign much importance to the presence of *Pityoxylon Chasense* in the Permian and to the supposed occurrence of *P. Conwentzianum* in the Carboniferous, as indicating the great geological age of the Abietineae. They state (p. 13):

> The *Pityoxylon Conwentzianum* of GOEPPERT from the Carboniferous of Waldenburg, which has often been called in question, has received full confirmation from the description of a similar type of *Pityoxylon, P. Chasense*, by PENHALLOW, from the Permian of Kansas. In these two species vertical resin canals are said to be absent, although the horizontal canals of the fusiform rays are clearly present. There is, accordingly, every reason to believe that the Abietineae are a very ancient group in their first appearance. In fact, they may be traced geologically quite as far back as the Araucarineae, which it is customary at the present time to regard as the oldest of the Coniferales.

More recently GOTHAN (**2**) has again "called in question" the authenticity of *P. Conwentzianum* as a Carboniferous form. He shows that this species whose horizon was never determined cannot, on structural grounds, belong to the Carboniferous. In this regard he refers (1) to the modern character of the radial pitting of the tracheids, which he has shown (**1**) is entirely lacking in all true Carboniferous woods; and (2) to the typical annual rings which are present, which are not found in any Carboniferous form. He also refers to the doubt expressed by Count SOLMS as to the validity of *P. Conwentzianum*, and to the fact that no more material of it can be found in the Carboniferous of Waldenburg, from which much wood is known. Finally, he again emphasizes the uncertainty as to the source and horizon of the material, which he states was found "auf eine Halde (!) des Waldenburgischen" (**2**, p. 22). No reliance can thus be placed on this form as indicating the presence of the Abietineae in the Carboniferous.

P. Chasense was described by the late Professor D. P. PENHALLOW in 1900 from material which was collected by C. S. PROSSER

from the "Chase Formation (Permian) at Coon Creek, Chase Co., Kansas, in 1897" (PENHALLOW **5**, p. 76). The type set of sections is the property of the Peter Redpath Museum, and through the courtesy of the McGill authorities has been put at our disposal for study. It is to be regretted, however, that no more material of the specimen from which the sections were prepared can be found. Careful search has been made both at McGill and at Washington (U.S. Geological Survey), where PROSSER sent his collection. The sections are three in number, transverse, radial, and tangential. They are labeled "*Pityoxylon Chasense*, 5, Cretaceous,[1] C. S. Prosser." Plate figs. 1–3 show these at a low magnification. The matrix is siliceous, but the material is only "fairly well preserved," and though the sections have been excellently made, certain important structural features are not determinable. PENHALLOW'S description is very brief, and is not illustrated. This renders it difficult to correlate it with the sections.

The transverse section is 12.5 mm. in radial extent, and in that distance shows no growth rings, so that it seems probable that these are absent or at least poorly developed, as PENHALLOW has stated. This feature and the form and arrangement of the tracheids are shown in plate fig. 4. The absence of annual rings is not a characteristic of the genus *Pityoxylon* of KRAUS, and yet in spite of this, and in spite of other important features which indicate its cordaitean affinity, PENHALLOW placed this form under that genus, because of the occurrence of what he considered were horizontal resin canals.

Text fig. 1*A* illustrates the character of the medullary ray cells in radial section. They are four to five times as long as high, and, as compared with the tracheids, are thin-walled; the radial extent of the latter and the thickness of their walls are indicated by the sets of short lines below the parenchyma cells. Many rays were examined, but no pits could be found on either the horizontal or terminal walls, nor is there any special thickening of these walls, features which are characteristic of *Pityoxylon*. Their structure, on the contrary, is of the characteristic cordaitean or *Araucarioxylon* type.

[1] There would seem to have been an error in labeling these "Cretaceous," since the Chase formation is Permian, as PENHALLOW himself has stated in his description.

The radial pitting of the tracheids is illustrated in text fig. 1*B*, which is taken from the radial section at the place marked *d* in plate fig. 2. The bordered pits are "in 1–3 rows, chiefly 2 rows."[2] They are alternate in arrangement, and flattened, as it were, by mutual contact, often presenting a more or less hexagonal outline. The orifice is not "probably round," however, though such appearances are quite common where the preservation is defective (text fig. 1*C*).

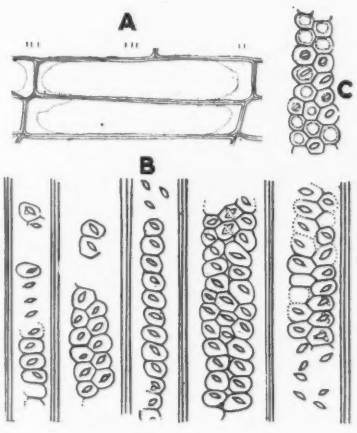

FIG. 1

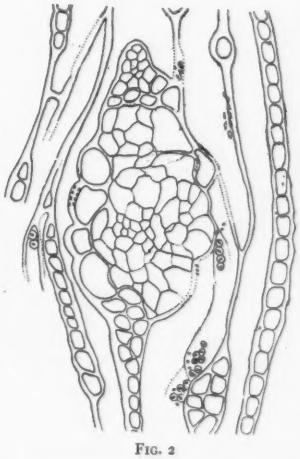

FIG. 2

FIGS. 1–2.—Fig. 1, from radial cross-section: *A*, medullary ray cells; *B*, radial pitting of tracheids (from plate fig. 2 at *d*); *C*, radial pitting in poor state of preservation; ×250; fig. 2, from tangential section (plate fig. 3 at *a*): showing tissue continuous and also tangential pitting adjacent to the ray; ×100.

Even here transitions to the normal type can be observed. It is elongated and obliquely placed, the two orifices on contiguous walls in some cases showing at right angles to one another (first and second tracheids from the right in text fig. 1*B*). This is not the character of the radial pitting of *Pityoxylon* as defined by KRAUS (SCHIMPER and SCHENCK **6,** p. 852), "Aréoles uniséries; opposées lorsqu'il y en a deux rangs," but that of an *Araucarioxylon* or cordaitean form.

The presence of horizontal resin canals upon which "*P. Chasense*" is referred to the genus *Pityoxylon* is exhibited, according

[2] Fifty counts were made in different parts of the radial section with the following result: 1-seriate 16 per cent, 2-seriate 62 per cent, and 3-seriate 22 per cent.

to PENHALLOW, "in the tangential section only, probably in consequence of the special condition of preservation," though what that "special condition" may be when the sections are all made from the same block is not evident. This feature, however, is considered important enough, in spite of the above described cordaitean features, to "separate the plant from *Cordaites*, and its affinities are rather with the *Pityoxylon* of KRAUS."

In the tangential section there are four broad medullary rays (plate fig. 3, *a*, *b*, *c*, *d*) with their tissues in a fair state of preservation, the two best preserved of which are shown in figs. 6 and 7. There are also traces of two more. PENHALLOW'S description of these is "fusiform rays, the terminals linear and of the structure of the uniseriate rays; the central tract very broad, nearly round; the cells large, thin-walled, irregular, and enclosing a small central resin passage with large epithelium cells." The writers have examined all these rays carefully, and the sketch (text fig. 2) was made after a prolonged study of the best preserved one (fig. 6). The camera lucida was used to outline this, but a few details were added afterward. It shows the tissue continuous from side to side of the ray, neither could there be found in this nor in any of the others a trace of a "small, central resin passage with large epithelium cells." Fig. 7 shows the only one that could be considered to have anything resembling a resin canal in it, and it was found by the use of the polariscope that the two darker areas (*a* and *b*) in this were due to aggregates of crystals of silica. Partial outlines of the crystals appear in the photograph.

Since the writers could find no evidence of resin canals in these large fusiform rays, it became interesting to know their real character. A significant feature in this connection is the irregularity of their margin, which is very different from that found in rays in the pines with horizontal resin canals, or even in such abnormal cases as those of *Sequoia Penhallowii* (JEFFREY 3). Around the rays, moreover, there is a considerable amount of tangential pitting on the tracheids (text fig. 2), a feature which is not found in any form known to the writers in connection with rays which inclose resin canals. This, however, is a feature of medullary rays which contain leaf traces, and since we have found undoubted leaf

traces in the radial and transverse sections of *P. Chasense* in rays which are quite similar in size and structure to those in the tangential section (cf. plate figs. 6 and 7 with fig. 8), it is considered that these are identical with the fusiform rays described by PENHALLOW. In the radial section they pursue an almost horizontal course (plate figs. 2*a* [?] and *b*), as is the case in the old-wood of the Araucarineae. Further explanation need not be entered into here, since one of the writers is preparing a contribution to the character of the leaf trace in certain fossil and living conifers, in which this feature will be studied in detail.

Since, then, the so-called resin canals of "*Pityoxylon Chasense*" are proven not to be such, there is left no basis for calling this form a *Pityoxylon*. On the other hand, (1) the absence of annual rings, (2) the character of the ordinary medullary rays (1 to partly 2-seriate with cells of thin-walled unpitted parenchyma), and (3) the multiseriate, alternate, and hexagonal radial pitting of the tracheids afford clear indication of its cordaitean affinity. This form, then, instead of affording "full confirmation" (*op. cit.*, p. 1) of the authenticity of *P. Conwentzianum*, lends no support to it, but might rather be considered as emphasizing the insecurity of the evidence upon which, as GOTHAN has recently shown (see p. 1), the latter is referred to the Carboniferous. The claim for the great geological age of the Abietineae thus fails on critical study of both the Permian and the Carboniferous forms upon which it is based.

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DESCRIPTION OF PLATE XXVI

FIG. 1.—Transverse section in two parts (*a* and *b*); ×5.

FIG. 2.—Radial section: at *a*, a possible branch; at *b*, a leaf trace cut longitudinally; at *c*, one cut obliquely; and at *d*, the pitting shown in text fig. 1*C*; ×5.

FIG. 3.—Tangential section: *a*, *b*, *c*, *d* are the fusiform rays; ×5.

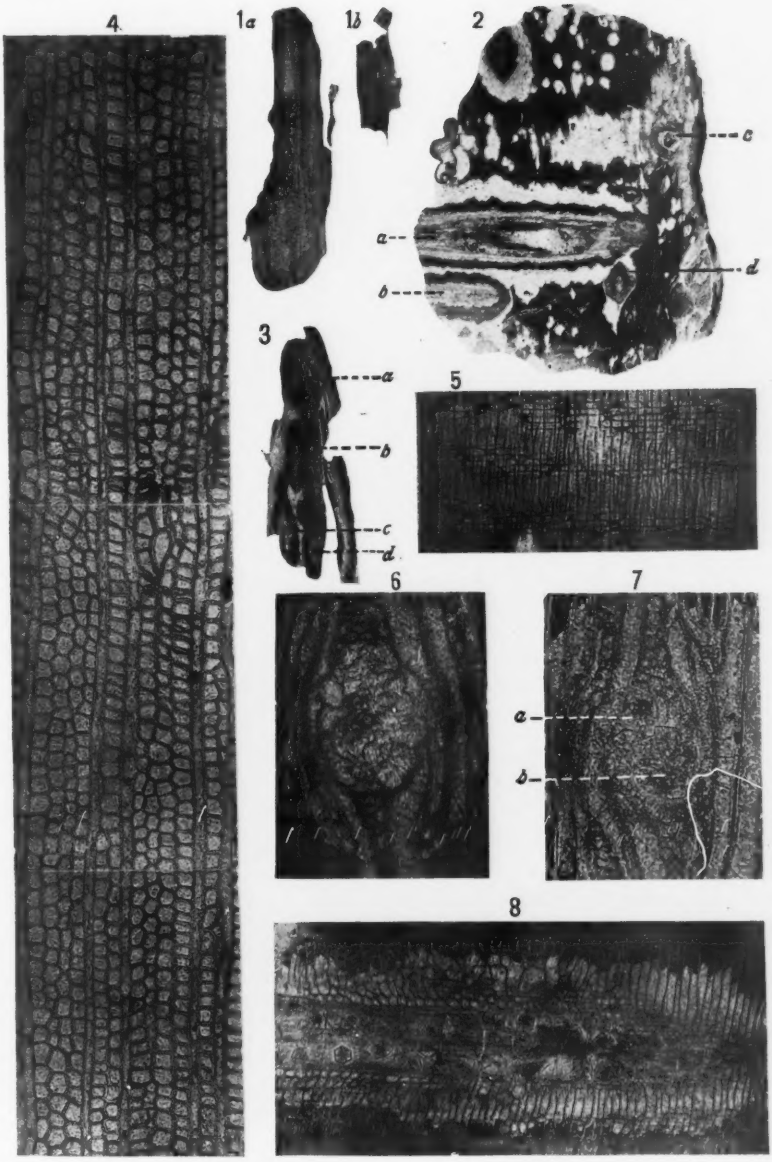
FIG. 4.—Transverse section: showing tracheids and medullary rays with no annual rings; the figure is from three photographs combined; ×80.

FIG. 5.—Radial section of medullary rays; ×40.

FIG. 6.—Tangential section of best preserved medullary ray (*a* in fig. 3) from which text fig. 2 was drawn; ×80.

FIG. 7.—Tangential section of a medullary ray (*d* in fig. 3) with two aggregates of crystals of silica in it at *a* and *b*; ×80.

FIG. 8.—Radial section of the leaf trace, from fig. 2*b*; ×40.



THOMSON & ALLIN on PITYOXYLON

BRIEFER ARTICLES

SUSAN MARIA HALLOWELL

(WITH PORTRAIT)

SUSAN M. HALLOWELL was born in Bangor, Maine, on August 25, 1835, and died December 15, 1911, at Wellesley, Massachusetts. From childhood Miss HALLOWELL loved study and was a lover of nature. She began her profession of teaching as soon as she was graduated from the high school. At that time institutions for the higher education of women were unknown. For more than twenty years she taught in the Bangor high school, continuing, as best she could, her self-education. But her thirst for knowledge could not be thus slaked. She longed to come into touch with the great masters of thought, and so, while still a teacher in the high school, she found her way into the laboratories of AGASSIZ and of ASA GRAY. These educators recognized the rare genius and power of this young woman, and it was through their recommendations that, in 1875, she was appointed Professor of Natural History in Wellesley College almost before the corner-stone of the first building of the new college was laid.

With that indefatigable zeal so characteristic of her whole life, she began the work in preparation for the new position. She went from college to college, from university to university, studying the scientific libraries and laboratories. At the close of this investigation she

announced to the founders of the college that the task which they had assigned her was too great for any one individual to undertake. There must be several professorships rather than one. Of those named she was given first choice, and when in 1876 she opened her laboratories and actually began her teaching in Wellesley College, she did so as Professor of Botany, although her title was not formally changed until 1878.

As soon as the newly founded department could be spared her immediate guidance, she went to Europe for further study. Here again she found the universities closed to women students. In that quiet but persuasive manner so characteristic of her, she applied for admission to the University of Berlin, and was the first woman to be admitted to the botanical lectures and laboratories of that university. At the age of 67, Miss HALLOWELL retired from active service in the college and was made Emeritus Professor of Botany, in February 1902.

Professor HALLOWELL was a pioneer in the higher education of women, the first and only woman to have organized and maintained at a high degree of efficiency, for more than twenty-five years, a department of botany. The foundations which she laid were so broad and sure, the several courses which she organized were so carefully outlined, that, except where necessitated by more recent developments in the science, only very slight changes in the arrangement and distribution of the work in her department have since been necessary. In addition to the providing of general equipment of the laboratories, much time was devoted to the development of the herbaria and to the securing of other illustrative material. She organized and built up a botanical library which from the very first was second to that of no other college in the country, and is today only surpassed by the botanical libraries of a few of our greatest universities. With an enthusiasm that never failed, and a persistence that knew no defeat, she gave herself to the working out of her ideals in scholarship and in life.

Gentle and dignified in manner, sympathetic and generous of heart, rich in her knowledge of nature, with a rare felicity of expression, and with that humility and reverence which characterize the true lover of nature, she inspired and enriched the lives of her pupils and associates.

Professor HALLOWELL was not a productive scholar, as that term is now used, and hence her gifts and her achievements are but little known to the botanists of today. She was pre-eminently a teacher and an organizer. Only those who knew her in this double capacity can fully realize the richness of her nature and the power of her personality. Her work will not be immortalized in cold bibliographies, neither will it be

writ alone in the hearts of those for whom and with whom she labored, for she touched life to nobler issues. With her death there has passed from us another of that constantly diminishing group of rare students and teachers who have contributed so largely to the dignity and permanency of higher education in America.—MARGARET C. FERGUSON.

TWO EPIPHYTIC ALGAE: A CORRECTION

Mr. J. H. BARNHART, through the editor of the BOTANICAL GAZETTE, has called attention to a possible difference in opinion in regard to the correctness of the name *Pirulus gemmata* given to a new genus of algae described in this journal.[1] When the name was selected, the writer was aware of this possible difference in interpretation, but the form was chosen which seemed to her to be most appropriate. On submitting the question to several authorities, however, the consensus of opinions seems to be that the name should read **Pirula gemmata** instead of *Pirulus gemmata*, and the writer would like to make this change.

Attention was also called by Mr. BARNHART to a mistake in the name *Aeronema polymorpha*, which should read **Aeronemum polymorphum.**—JULIA W. SNOW, *Smith College, Northampton, Mass.*

[1] SNOW, JULIA W., Two epiphytic algae. BOT. GAZ. **51**: 360–368. *pl. 18.* 1911.

CURRENT LITERATURE

BOOK REVIEWS

British vegetation

In two respects, at least, the appearance of *Types of British vegetation* marks an epoch in the development of plant geography.[1] In the first place, the publication of the volume at this time is due to the organization of an International Phytogeographic Excursion in the British Isles during the summer of 1911. The volume was prepared in anticipation of this excursion, and advance copies were presented to the members of the party. The chief result of this excursion has been to internationalize for all time the subject of plant geography, and to divest it of the provincialism which has hitherto too greatly characterized it. Besides marking the initiation of internationalism in phytogeography, this volume marks another great advance, namely, the study of vegetation by an organization rather than by an individual. While edited by TANSLEY, the volume was gotten together by the "Central Committee for the survey and study of British vegetation," more popularly known as the "British vegetation committee." It is not so long ago that the study of vegetation played an insignificant part in British botany. Through the work of their vegetation committee, the British not only have caught up with their American and continental brethren, but, in organization at least, they have forged ahead.

The introduction deals with the units of vegetation, following the general lines marked out previously by Moss.[2] While all plant geographers seem to believe in the reality of the terms formation and association, and to believe that the formation should be used as the larger unit, including various smaller units or associations, it is evident from this book, as from the discussions of the 1911 excursion, that the British plant geographers differ radically from all others in the practical application of these terms. For example, calcareous soils are regarded as having a single formation, which includes such diverse things as limestone-pavement associations with almost bare rock surface, limestone grassland, limestone scrub, chalk heath, yew woods, ash woods, and beech woods. Similarly the sand-dune formation is composed of strand associations, morrain-grass and couch-grass associations, dune grassland, dune scrub with willows, and dune marshes. The reviewer has shown that on the sand dunes of Lake Michigan there is to be found nearly every kind of plant formation characteristic of the region, from the xerophytic vegetation of the

[1] TANSLEY, A. G., with various collaborators, Types of British vegetation. pp. xx+416. *pls. 36. figs. 21.* Cambridge: University Press. 1911.

[2] See BOT. GAZ. **52**:321. 1911.

moving dunes or the swamp vegetation of the dune depressions to a mesophytic climax forest of beech and maple. By the British concept all of these are to be considered as composing a single formation! It must be admitted that the British concept of formation is the most workable yet proposed, for it represents in essence the aggregate of plant associations which compose a successional series on a given habitat. It must be admitted also that those who oppose the British concept are not agreed among themselves, when it comes to actual field discriminations between associations and formations. However, the British concept proposed by Moss and adopted by the committee, represents a most radical departure from all past formational concepts, and seems to be out of harmony with the proposals internationally agreed upon in Brussels in 1910.

Whatever may be said concerning concepts and modes of classification, nothing but praise can be rendered for the detailed presentation of British vegetation. The editor presents the chapter on British climate, as well as a part of that on the soil; W. G. SMITH gives the part on Scottish soils, and G. A. J. COLE that on Irish soils. Following a description of the general distribution of British vegetation by the editor is an account of the plant formation of clays and loams, also by the editor. The chief association here is that dominated by *Quercus pedunculata*, with an undergrowth dominated by the hazel. This formation includes also retrogressive associations of scrub (dominated largely by Rosaceae) and grassland. The editor contributes also the chapter on the formation of sandy soil. The chief association is that of oakwood, in which *Q. sessiliflora*, as well as *Q. pedunculata*, is a prominent member. The chapter on the heath formation is presented as a whole by the editor, the part on Scottish heaths being contributed by W. G. SMITH. As was well shown at various points in the 1911 excursion, the heath often has originated retrogressively through the degeneration of woodland. The first step in such retrogression appears to be the invasion of oakwood by birch and heather; after a time the heath may become dominant. The heath in time may be invaded by pine or birch, illustrating progressive succession.

Most of the chapter on formation of the older siliceous soils is contributed by Moss. The chief association is an oakwood dominated by *Q. sessiliflora*. Retrogression from forest through scrub to grassland is well illustrated in this formation. The splendid oak woods of Killarney, with their Mediterranean components, notably *Arbutus Unedo*, are classed here; the Killarney forest proved to be one of the most fascinating areas visited by the 1911 excursionists. In the preparation of the extensive and interesting chapter on the formation of calcareous soils, the editor was aided by Moss and also by W. M. RANKIN. Three subformations are here recognized, that of the older limestones, that of the chalk, and that of the marls and calcareous sandstones. The first is presented by Moss, who also conducted the excursion to the Derbyshire dales, where it is well illustrated. The chief association is dominated by the ash, *Fraxinus excelsior*, and retrogressive stages to scrub and later to

grassland are frequently observed. A remarkable association is that of the limestone pavements, such as the 1911 party visited in western Ireland; these areas have much bare rock surface, and a most interesting vegetation, largely mesophytic, is all but hidden in deep crevices. The chalk hills or downs, while resembling the older limestones, are characterized more by beech woods than by ash woods, though the latter are sometimes found. Another interesting type of the chalk is the yew woodland.

The chapter on aquatic vegetation is by the editor, except for the part on the plankton, which is contributed by G. S. WEST, and the part on quickly flowing streams, which is contributed by MOSS. Short chapters follow on the marsh formation and on the vegetation of peat and peaty soils, both by the editor. Miss PALLIS, the efficient guide of the 1911 excursion in the Norfolk Broads, contributes a chapter on the aquatic and fen formations of that region. This chapter presents a district as a unit, the consideration of the physiographic development of the area being followed by a treatment of the aquatic formation and the fen formation with its various associations, and by a discussion of the genetic relationships of the associations involved.

Two chapters are devoted to the moor formation, the lowland moors being presented by the editor, assisted by RANKIN, and the upland moors by F. J. LEWIS, C. E. MOSS, and W. G. SMITH. RANKIN, who conducted the 1911 party to some of the Lancashire moors, considers the latter under the two heads of estuarine and lacustrine moors, the former being much the more extensive. While the heather, *Calluna vulgaris*, generally dominates the successional series, here it seems to culminate in a birchwood, but there are many examples of retrogression to heather moorland with birch stumps buried *in situ*. RANKIN considers also the valley moors of the New Forest, which were visited from Portsmouth at the close of the excursion. Upland moors were seen frequently during the course of the excursion, the foreign guests being repeatedly surprised at their vast extent, especially in habitats which in most parts of the world would be forested. That these were once forested, at least in part, was made evident again and again by the discovery of forest layers buried in the peat. Over vast areas the dominant plant of the upland moors is a cotton grass, *Eriophorum vaginatum*. In some places, especially in Scotland, there are extensive grass moors. Denudation and retrogression are frequently conspicuous.

The chapter on arctic-alpine vegetation is presented by W. G. SMITH, who was the chief guide of the party in Scotland. The discussion is devoted chiefly to Ben Lawers, which was visited by the excursionists. The delimitation of formations here is more in harmony with that employed by most writers, the author distinguishing three formations near the summit: the arctic-alpine grassland formation, the formation of mountain top detritus, and the formation of arctic-alpine chomophytes (i.e., plants of rock ledges and fissures). The final chapter, prepared chiefly by the editor, considers the vegetation of the sea coast, the chief formations recognized being the salt

marsh and the sand dune. The composition of the various associations and the trend of succession are like those of the Continent and are familiar through the work of WARMING, MASSART, and other writers. Perhaps the most unique feature of the British coast is afforded by the shingle beach communities, which are most ably treated by OLIVER, who conducted the 1911 party to his seaside laboratory at Blakeney, where these communities are well developed. The most striking feature here is the presence of a shingle or gravel dune, which invades the marshland and presents conditions resembling in many ways the more familiar phenomena of sand dunes.

The photographic illustrations in this volume are notably well selected, and most admirably reproduced, and are supplemented by a few instructive diagrams. The British vegetation committee may well be proud of their record for 1911. It is to be hoped and expected that such books as the one here reviewed, and such phytogeographic excursions as the one here mentioned, will hereafter be frequently recurring features of phytogeographic progress.—H. C. COWLES.

The soil solution

Those plant physiologists who are interested in the subterranean surroundings of plants and in the relations which obtain between soil conditions and plant activity will welcome CAMERON'S little book entitled *The soil solution*.[3] The treatment is exceedingly clear and concise, logically arranged, and very readable. Furthermore, it is unquestionably the best and most scientific treatise on this difficult yet most important subject which we have seen. The author originally approached the soil problems from the standpoint of the chemist, developing their biological and agricultural aspect according to the demands of researches under his direction, and perhaps this fact has left a mark upon some of his discussions which may seem novel to the reader coming to this field from a specifically botanical training. But the novel features of the author's treatment may be regarded as quite in line with the recent trend of physiology toward a quite uncolored physical treatment.

Another group of workers whose attitude toward plant happenings is often not that of the physiologist, and whose activities have been mainly directed toward the empirical acquisition of more or less superficial principles and relations, will read CAMERON'S contribution with much interest, perhaps even with excitement. We refer here to students of practical agriculture, who will find here that some of the most widely accepted hypotheses of this field are clearly discredited. This will not be at all surprising, however, to him who has followed the recent literature, for the previous publications of the author and his colleagues have given, from time to time, the main features of the researches upon which his present attitude toward soil science has been built up. During

[3] CAMERON, FRANK K., The soil solution, the nutrient medium for plant growth. pp. v+136. *figs.* 3. Easton (Pa.): The Chemical Publishing Co. 1911.

the past decade we have received many quite novel propositions and suggestions from this group of workers, most of which were read with greater or less lack of conviction by agricultural scientists. With the advance of time, however, most of these new ideas have continually gained ground throughout the world.

Aside from its general value as an example of an exceptionally rational study of a very complex and difficult set of natural relations, the keynote of the present book is perhaps suitably expressed by the following sentence taken from p. 17: "Just as the phlogiston theory passed away when the elementary nature of oxygen was established and LAVOISIER taught the scientific world to use the balance, so the plant food theory of fertilizers must pass with increasing knowledge of the relation of soil to plant and the application of modern methods of research to the problem."

It is emphasized throughout that the problems here involved are dynamic; that the soil, as well as the plant, are the seats of continuously changing chemical and physical processes; thus no static interpretation of the environment of roots is of much avail, and the general failure of soil analyses to answer the fundamental question with which we are concerned seems to have been due to the failure of such methods to bring out the dynamic nature of soil phenomena. A chapter is devoted to a somewhat thorough discussion of the concentration and the nature of the mineral solutes of the soil solution, with reference to the conditions which control these features and keep them in constant change, always tending toward equilibrium but probably seldom attaining it. Then follows a discussion of soil absorption, with a clear setting forth of the logical fallacy of the prevalent interpretation of apparent soil acidity.

In the chapter on "The balance between supply and removal of mineral plant nutrients," MCGEE's startling series of terms ("run-off," "cut-off," "fly-off") to denote the superficial and subterranean drainage and the loss by evaporation, respectively, from the soil has been adopted. The reviewer can see so little tendency of modern serious English to revert to this fundamentally Teutonic style of etymology that he cannot but look askance at these last two newly coined expressions. This chapter is the weakest in the book, and most readers will feel that the question "Is the movement of mineral plant nutriments toward the surface soil equal to or in excess of the removal by drainage waters and garnered crops?" (p. 75) is not answered with data or considerations which even "appear sufficient for the present purpose." The approximations given of the number of tons of potassium, etc., annually carried, in the United States, toward the soil surface, removed by crops, and washed into the sea are of no interest as regards any particular plant or soil. The question must be settled with reference to particular soil areas, by experimental studies yet to be accomplished. However, the author is quite aware of the weakness of these calculations, and admits that "it is wise to avoid giving them too much emphasis." His thesis against the LIEBIG theory of fertilizer action gets its support from quite different lines of argument.

In the chapter on "The organic constituents of the soil solution" is given a convincing account of the toxic substance theory of soil fertility. Any treatment of an organically poisoned soil, which will increase its absorptive properties or its oxidizing power seems to have a beneficial effect upon plants growing therein. The commonly used fertilizer salts are often effective in this way, so that there is nothing in the new theory which might lead one *not* to use the ordinary fertilizers prescribed by the "plant food" theory. This more recent finding of the Bureau of Soils makes the violent and often personal attacks, that have been calculated to hinder the progress of these investigations, appear largely as the mere pommelling of a man of straw.

The book ends with a chapter on the phenomena of alkali soils, dealing with the development of alkali and the theory of its practical handling.—B. E. LIVINGSTON.

Fossil plants

In the second volume of his *Fossil plants*, Professor SEWARD[4] continues the work begun over ten years ago and apparently destined to become truly monumental. It is to be hoped that his anticipation of the early appearance of the third volume on the gymnosperms may be realized, and that a fourth hinted at, rather than promised, which is to deal with the angiosperms, may likewise soon be published. The author brings very unusual qualifications to the titanic task of writing a comprehensive textbook of the present condition of our knowledge of fossil plants in both their botanical and geological bearings. He possesses in an unusual degree an acquaintance with the older paleobotany, dealing mainly with the superficial features of plants as seen in impressions, and at the same time is thoroughly in touch with the modern development of the subject, which has put the study of internal structure in the foreground. It is to be regretted that some of the younger investigators of fossil plants are often deplorably ignorant of the older point of view. SEWARD certainly does not err in the direction of the neglect of the older literature or superficial features, which in many cases constitute the only evidence available. Another advantage enjoyed by the author is his unique first-hand knowledge of the material treated. By his travels to various paleobotanically interesting regions and by personal visits to most of the important European collections, he has acquired an intimate acquaintance with fossil plants in their fullest systematic, geological, geographical, and evolutionary bearings possessed by no other living paleobotanist.

The present volume continues the treatment of the Pteridophyta begun in the first, which appeared over ten years ago. In the preface he points out the happy circumstance that recent activity has been chiefly in the field of the present volume, and that as a consequence the first is little out of date. Beginning with a continued discussion of the Sphenophyllales, the writer subscribes a very

[4] SEWARD, A. C., Fossil plants. Vol. II. pp. xxii+624. *figs. 265*. Cambridge: The University Press. 1910.

qualified adherence to the views expressed in recent years in England, as to the affinity of the Psilotales with this phylum. The genus *Psilophyton*, established by the late Sir WILLIAM DAWSON of McGill University, for forms from the Devonian of eastern Canada and of Scotland supposed to be allied to the living *Psilotum*, is critically examined and rejected as being based on insufficient evidence.

The Lycopodiales are considered in 250 well-illustrated pages. Beginning with the superficial and anatomical characters of the living representatives of the group, the author, in common with all paleobotanists of standing, rejects the idea that the genus *Isoetes* has filicinean rather than lycopodineous affinities. This suggestion, first made by an English plant physiologist, seems now to be finally disposed of. The fossil Lycopodiales are discussed under the convenient captions of Isoetaceae and Pleuromeia, herbaceous fossil Lycopodiales, and arborescent Lycopodiales, a special chapter being added on those remains which the author frankly designates seed-bearing Lycopodiales.

The Filicales or fernlike Pteridophyta, together with a number of apparently allied forms, concerning which it is yet uncertain whether they are true ferns or merely fernlike seedplants, occupy the remaining and larger part of the volume. The treatment of the fossil Filicales begins with a comprehensive anatomical and systematical account of their still living allies. The anatomical treatment, as might be expected, is characterized by a decided "insularity," the views of GWYNNE-VAUGHAN, BOODLE, and other English anatomists being unhesitatingly adopted. The chapters on fossil ferns contain such a well-digested wealth of material that it is quite impossible to summarize them or even indicate their tendency in this necessarily brief review. It is enough to say that they constitute a particularly valuable part of the present volume and represent a region of the fossil field where the author is peculiarly at home.

If the work of which the volume under consideration constitutes such an important fraction is completed, as is devoutly to be desired, it will be the most complete and thoroughly modern work on the subject, and will serve to replace the now somewhat antiquated botanical part of ZITTEL'S well-known *Handbuch*, compiled by SCHIMPER, SCHENK, KRAUS, and others. It is lightened and vitalized by the comparison of external and internal features of the various fossils treated, with the similar forms still living. By this method the reader, whether he be botanical or geological in his interests, acquires a vivid picture of the evolutionary sequence of plants in the history of our world.—E. C. JEFFREY.

MINOR NOTICES

Bulletin du Jardin botanique de Buitenzorg[5] is the title resumed by the Botanical Gardens of Buitenzorg to take place of the well-known serial "Bulletin du Département de l'agriculture aux Indes néerlandaises." The

[5] Bulletin du Jardin botanique de Buitenzorg. Deuxième série. No. I, pp. 29, *pls.* 4, August 1911. No. II, pp. 29, October 1911.

two numbers issued recently contain articles on Malayan ferns and Papuan orchids by eminent specialists. Several of the species included are new to science.—J. M. GREENMAN.

Handbook of deciduous trees.—The eleventh part (sixth section of second volume) of SCHNEIDER's *Handbook* has appeared,[6] following the preceding part in the same year. As stated in preceding notices, it contains descriptions, with illustrations, of the angiospermous trees of central Europe, both native and under cultivation. The present part begins with the completion of *Viburnum* and ends with *Fraxinus*.—J. M. C.

Flora of Jamaica.[7]—Of the numerous publications concerning West Indian botany which have appeared in recent years, it is doubtful if any has combined so successfully a scientific and semipopular treatment as the present volume. It concerns the Orchidaceae only, and is the result of years of observation of living plants, supplemented by the study of a large amount of herbarium material, particularly the collections in the British Museum, in the Kew Herbarium, and in the Herbarium of the government of Jamaica.

The total number of genera constituting the orchid flora of Jamaica is given as 61, and to these are referred 194 species. One genus, *Homalopetalum*, and 73 of the recognized species are said to be confined to the island. The strongest affinity of the orchid flora is said to be with Cuba, as shown by the fact that 82 out of the 121 species, which are not endemic, occur in Cuba, and 14 of these are restricted to the two islands. The book is attractive in appearance, the keys concise, the synonomy ample but not cumbersome, the descriptions clear, and exsiccatae are very fully cited; moreover, the text is amplified by 32 full-page plates, illustrating all the genera represented, so that the book will be helpful to those interested only in living orchids, as well as to those occupied with the study of herbarium material. The authors state "it is proposed that the present volume shall form the first part of a complete *Flora of Jamaica*." It is earnestly hoped that the proposed work may be carried to completion.—J. M. GREENMAN.

New England trees in winter.—Books of a popular or semi-scientific type dealing with our native trees are already more than sufficiently abundant, and yet it is safe to say that the present volume by BLAKESLEE and JARVIS[8]

[6] SCHNEIDER, C. K., Illustriertes Handbuch der Laubholzkunde. Elfte Lieferung (sechste Lieferung des zweiten Bandes). Imp. 8vo. pp. 657–816. *figs. 420–514*. Jena: Gustav Fischer. 1911. *M* 5.

[7] FAWCETT, WILLIAM, and RENDLE, ALFRED BARTON, Flora of Jamaica, containing descriptions of the flowering plants known from the island. Vol. I. Orchidaceae. 8vo. pp. xviii+150. *pls. 32*. London: British Museum (Natural History). 1910.

[8] BLAKESLEE, A. F., and JARVIS, C. D., New England trees in winter. Storrs Agricultural Exper. Sta. Bull. 69. pp. 269. *pls. 109*. 1911.

will be welcomed on its merits both by botanists and by the general public. It consists of an introduction of an elementary character discussing the general problems of tree growth and illustrating some of the technical terms employed, a key for the determination of species on the basis of leaf and bud characters, supplemented by additional keys for the chief genera, and illustrated descriptions of over 100 species found in New England. This list includes not only all that are native to the region, but in addition the species that are commonly grown for ornamental purposes, thus extending the usefulness of the volume to the study of the trees of city parks and of areas far beyond the limits designated in the title of the volume.

One page is devoted to the description of each tree, while facing the description is a plate illustrating the species in winter condition. These plates contain reproductions of photographs of the general habit, the trunk, showing bark characters, the twig with buds and leaf scars, and the fruit. They are so uniformly excellent in quality that they must be regarded as the best collection of illustrations of the sort that have yet appeared. By their aid almost all common trees may be recognized readily by the ordinary reader. The descriptive text is wonderfully complete when its brevity is considered. Synonyms of both popular and scientific names are given, followed by separate paragraphs on the habit, bark, twigs, leaf scars, buds, fruit, wood, distribution, and comparisons with other species. Such an arrangement of material makes the manual well adapted for ready reference. As a manual it should be a valuable addition to those already available for college classes, but it is likely to prove even more valuable to teachers in public and high schools who are attempting to lead pupils to become familiar with our native trees. In addition to its present form, its authors indicate their intention of publishing it as a book, thus making it more widely available.—GEO. D. FULLER.

British liverworts.—In the prefatory note to a little volume on liverworts[9] the authors say that the book is intended to be a companion volume to their essay on *British mosses*. It is sincerely hoped that it will always remain on the shelf with that volume, and not fall into the hands of isolated students who are trying to get accurate information about liverworts. A few quotations will show what the authors know about the group as well as botany in general. "The liverworts present to one's mind the idea of a crowd of organisms which have not made up their minds in which line they shall go, and are trying experiments in all directions to see what is best for them to take." The following statement will be interesting to morphologists and physiologists: "A marked peculiarity of the thallus [of *Anthoceros*] is found in the manner in which the coloring matter is disposed. In some cells the chlorophyll may be seen gathered round the cell walls, either forming a continuous line or as separate

[9] FRY, EDWARD and AGNES, The liverworts, British and foreign. pp. viii+74. *figs. 49*. London: Witherby & Co. 1911.

bodies, but other cells, instead of possessing many diffused grains of chlorophyll, have a so-called chloroplast, a large flattened plate of coloring matter which incloses the nucleus." Of *Marchantia* we read: "Below and between each pair of rays the disk bears a perichaetium, i.e., the wrapper or involucre of a sporogone or female cell, which when fertilized by an antherozoid produces a mass of cells accompanied by elaters. The archegone itself thus becomes the spore case. These female organs are variously known as disks, receptacles, or inflorescences." Again, "On the upper surface of the thallus of *Pellia* may be seen, in both spring and autumn, small dots on either side of the midrib. These are very minute globular bodies attached by a slight thread to the subadjacent tissue. These bodies are known as antheridia or antherids, and may be compared with the stamens of flowering plants. From each antherid comes at maturity a mass of small spiral bodies, known as antherozoids (or spermatozoids), which may be compared with and play the part of the pollen of a flowering plant." Using *Pellia epiphylla* as an example, we find that "if we start with a spore, we shall find that it produces a thallus on which grow the archegones and the antherids, which by their union produce a fertilized ovum." There are many more such statements in the little book.—W. J. G. LAND.

NOTES FOR STUDENTS

Current taxonomic literature.—S. ALEXANDER (Rep. Mich. Acad. Sci. **13**:191–198. 1911) records the results of a continued study of the perennial species of *Helianthus*. The author finds distinguishing characters in the underground parts of sunflowers and incorporates these characters in a tabular synopsis of the Michigan species.—G. BEAUVERD (Bull. Soc. Bot. Genève II. **3**:253–260. 1911) under the title "Contribution a l'étude des Composées" has proposed a new genus (*Parantennaria*) founded on an Austrian species, *Antennaria uniceps* F. v. Müller.—O. BECCARI (Philip. Journ. Sci. Bot. **6**:229, 230. 1911) gives a list of plants of the island of Polillo, describing a new species of *Livistona* (*L. Robinsoniana*) and two new varieties in the genus *Areca*.—E. P. BICKNELL (Bull. Torr. Bot. Club **38**:447–460. 1911) in an eighth article on "The ferns and flowering plants of Nantucket" records further noteworthy plants and characterizes a new species of *Amelanchier*.—G. BITTER (Bot. Jahrb. **45**:564–656. *pls. 4–10*. 1911) has published a revision of the South American genus *Polylepis*, recognizing 33 species, 14 of which are new to science; the group has its greatest specific diversity in the north Andean region.—N. E. BROWN (Bot. Mag. *t. 8402*. 1911) describes and illustrates a new species of *Cladium* (*C. pubescens*) from Peru.—E. B. COPELAND (Leafl. Phil. Bot. **4**:1149–1152. 1911) describes 6 new species of ferns from the Philippine Islands.—S. T. DUNN (Kew Bull. 1911:362–364) has published a new genus (*Ostryoderris*) of the Leguminosae from tropical west Africa. The same author (Philip. Journ. Sci. Bot. **6**:315–317. 1911) gives a synopsis of the Philippine representatives of the genus *Milletia*, recognizing 11 species of which 3 are new to

science.—P. DUSÉN (Archiv för Botanik **10**:no. 5. 1–5. *pl. 1.* 1911) describes and illustrates a new species of *Eryngium* (*E. ombrophilum*) from Brazil.—W. R. DYKES (Gard. Chron. III. **51**:18. 1912) has published a new species of *Iris* (*I. tenuissima*) from California.—E. L. EKMAN (Archiv för Botanik **10**:no. 17. 1–43. *pls. 1–6.* 1911) under the title "Neue brasilianische Gräser" has published 19 species new to science and proposes a new genus (*Steirachne*) based on *Festuca pilosa* Nees.—A. W. EVANS (Rhodora **14**:1–18. 1912) publishes the ninth article of a series devoted to New England Hepaticae; up to the present time 169 species of this group have been recorded from the New England states.—F. W. FOXWORTHY (Philip. Journ. Sci. Bot. **6**:231–287. *pls. 34–44.* 1911) presents an article entitled "Philippine Dipterocarpaceae," recording important data concerning this family and enumerating about 40 species, of which 4 have not been described hitherto.—R. E. FRIES (Kungl. Svensk. Vetensk. Akad. Handl. **46**:no. 9. 1–72. *pls. 1–7.* 1911) presents the results of a monographic study of the genus *Petunia*, recognizing about 30 species of which 12 are new to science.—J. S. GAMBLE (Philip. Journ. Sci. Bot. **6**:289. 1911) publishes new species of *Schizostachyum* from Luzon, P.I.—J. M. GREENMAN (Ottawa Naturalist **25**:114–118. 1911) has published 4 new species and two varieties of Canadian Senecios.—A. A. HELLER (Muhlenbergia **7**:85–95. *pl. 6.* 1911) in continuation of his studies on the genus *Lupinus* records 3 new species from Oregon and California.—M. A. HOWE (Bull. Torr. Bot. Club **38**:489–514. *pls 27–34.* 1911), in a paper on "Some marine algae of Lower California, Mexico," records 24 species of which 8 are new.—J. HUTCHINSON (Hooker's Ic. IV. **10**:*pl. 2929.* 1911) describes and illustrates a new genus (*Protomegabaria*) of the Euphorbiaceae from tropical Africa.—E. JANCZEWSKI (Bull. Acad. Sci. Cracovie 1910: pp. 67–91) has issued additional supplements to his monograph of the Grossulariaceae and includes several hitherto unpublished species and varieties from China.—P. B. KENNEDY (Muhlenbergia **7**:97–100. *pl. 6.* 109–111. *pl. 8.* 1911) describes and illustrates a new clover (*Trifolium bolivianum*) from Bolivia and a new species of *Phlox* (*P. aciculifolia*) from Nevada.—F. D. KERN (Mycologia **3**:288–290. 1911) presents a second paper on "The rusts of Guatemala"; several species are recorded, including a new *Uromyces* parasitic on *Gouania domingensis* L. The same author (Bull. N.Y. Bot. Gard. **7**:391–483. *pls. 151–161.* 1911) under the title of "A biologic and taxonomic study of the genus *Gymnosporangium*" has published the results of a monographic study, recognizing 40 species of this genus.—K. KRAUSE (Bot. Jahrb. **45**:657–660. 1911) describes 6 new species of Araceae from the Philippine Islands.—J. LUNELL (Am. Mid. Nat. **2**:142–149, 153–164. 1911–1912) has described new species and varieties of flowering plants from North Dakota, Minnesota, and Florida.—R. MAIRE (Ann. Mycol. **9**:315–325. *pl. 16.* 1911) under the title "Remarques sur quelques Hypocréacées" has established a new genus (*Nectriopsis*) based on *Sphaeria violacea* Fr.—U. MARTELLI (Leafl. Phil. Bot. **3**:1109–1132. 1911) in an article entitled "Some Philippine Pandanaceae" has published 6 new

species of *Freycinetia* and 7 of *Pandanus*.—W. A. MURRILL (Mycologia **3**:271–282. 1911) in continuation of his work on the "Agaricaceae of tropical North America" treats seven genera with rose-colored spores, to which are referred 34 species, 21 of which are characterized as new. One new generic name is proposed, namely *Volvariopsis*, which is based on *Volvaria bombycina* (Schaeff.) Quél.—G. A. NADSON and A. G. KONOKOTINE (Bull. Jard. Imp. Bot. St. Pétersb. **11**:117–142. 1911) describe and illustrate a new genus (*Guilliermondia*) of the Saccharomycetes.—J. A. NIEUWLAND (Am. Mid. Nat. **2**:129–142. 1911) under the title "Box-elders, real and so-called" proposes a new generic name (*Crula*) for several Asiatic trees, which have been regarded by most authors as congeneric with *Acer;* the first-mentioned species under the newly constituted genus is *C. cissifolia* (*Negundo cissifolium* Sieb.).—L. QUEHL (Monats. für Kakteenk. **21**:154, 155. 1911) describes and illustrates a new species of *Mamillaria* (*M. Siedeliana*) from Mexico.—H. REHM (Ann. Mycol. **9**:363–371. 1911) has published 26 new species of American and Asiatic Ascomycetes.—B. L. ROBINSON (Proc. Am. Acad. **47**:191–216. 1911) in continuation of his studies in the Compositae has published upward of 20 new species and varieties, chiefly from tropical and subtropical America. The paper also includes several new combinations with complete synonomy, as the result of careful investigations of the generic affinity of formerly misplaced species.—C. B. ROBINSON (Phil. Journ. Sci. Bot. **6**:299–314. 1911) in a second article on "Philippine Urticaceae" records 6 hitherto undescribed species of this family, and (*ibid.* 319–358) under the title "Alabastra Philippinensia" has published about 30 new species belonging to different families of flowering plants.—E. E. SHERFF (Bull. Torr. Bot. Club **38**:481–482. *pl. 26.* 1911) places on record a new variety of *Carex* (*C. lupulina* var. *albomarginata*) from Michigan.—H. SOMMERSTORFF (Oester. Bot. Zeit. **61**:361–373. *pls. 5, 6.* 1911) in a paper entitled "Ein Tiere fangender Pilz" describes and illustrates a new genus (*Zoophagus*) the affinity of which seems to be with the Saprolegniales; the fungus was discovered in Styria, Austria.—O. STAPF (Bot. Mag. *t. 8405.* 1911) describes and figures a new species of *Phyllodoce* (*P. amabilis*) from North America. The same author (Hooker Ic. IV. **10**:*t. 2927.* 1911) describes and illustrates a new genus (*Heteranthoecia*) of the Gramineae from tropical Africa.—F. STEPHANI (Sp. Hep. **4**:417–464. 1911) in continuation of his work on the Hepaticae includes in the foregoing pages 112 species of *Trullania*, 48 of which are new to science.—F. STUCKERT (Anal. Mus. Nac. Bs. As. III. **14**:1–214. *pls. 1–4.* 1911) under the title "Tercera contribución al conocimiento de las graminácees Argentinas" records 369 species of grasses of which 20 are new. The identifications and the diagnoses of new species, varieties, and forms are by the eminent specialist Professor EDUARD HACKEL.—H. and P. SYDOW (Leafl. Phil. Bot. **4**:1153–1159. 1911) record 11 new species of fungi from the Philippine Islands.—H. and P. SYDOW and E. J. BUTLER (Ann. Mycol. **9**:372–421. *pl. 17.* 1911) under the title "Fungi Indiae orientalis" have recorded several new fungi and include the description of a new genus (*Meta-*

chora) of the Dothideaceae, found on the leaves of bamboo at Kanouth, Malabar.—A. WEBER VAN BOSSE (Ann. Jard. Bot. Buitenzorg II. **9**:25–33. 1911) under the title "Notice sur quelques genres nouveau d'algues de l'Archipel Malaisien" has published the following new genera: *Bryobesia* of the Chlorophyceae, *Mesospora* of the Phaeophyceae, *Exophyllum*, *Acanthochondria*, *Oligocladus*, and *Chalicostroma* of the Florideae, and *Perinema* of uncertain relationship.—H. F. WERNHAM (Journ. Bot. **49**:346. 1911) adds another new species from Costa Rica to the genus *Hamelia* recently revised by the same author.—A. ZAHLBRUCKNER (Ann. K. K. Naturhist. Hofmus. Wien **24**:293–326. *pls. 6, 7*. 1911) in cooperation with several specialists under the title "Plantae Pentherianeae" has published a list of plants collected in South Africa by Dr. A. PENTHER; the article includes a new genus (*Pentheriella* Hoffm. & Musch.) of the Compositae.—Different authors (Kew Bull. 1911:343–348) have published several species of flowering plants new to science of which 4 are from Mexico and South America.—J. M. GREENMAN.

Alternation of generations in Delesseria.—Alternation of generations among the red algae has begun to receive much attention, and a paper by SVEDELIUS[10] is one of the latest. The material for his investigation was collected at the Kristineberg Zoological Station, Bohnslän, Sweden, during November 1910. According to the account, in this species fertilization occurs in October, early in November the spermatangia are entirely washed off, tetraspore formation occurs in November, and both tetraspores and cystocarps mature during December and January. The time of his collection, therefore, was too late for securing material for sperm-formation and fertilization, so that there is no description of the male individuals of *Delesseria*, or of the development of procarp and fertilization.

The paper begins with an account of the development of tetrasporangia; then follow tetraspore formation, vegetative nuclear divisions in the tetrasporic plants, and vegetative mitosis in the female plants. Finally there is discussed the problem of alternation of generations in the Florideae. The nucleus of the tetraspore mother cell undergoes the tetrad division, which is preceded by synapsis and diakinesis. In the diakinesis stage 20 bivalent chromosomes are present; after both heterotypic and homotypic divisions, tetraspores are produced with 20 chromosomes; the vegetative nucleus of the tetrasporic plants has 40 chromosomes; and the vegetative nucleus of the female plants has 20 chromosomes. In the resting nucleus there are present chromatin granules whose number is much higher than the double number of chromosomes. In vegetative divisions some of these chromatin granules directly unite with one another and form chromosomes, with no appearance of a spirem thread period. In the heterotypic division all chromatin granules

[10] SVEDELIUS, N., Ueber den Generationswechsel bei *Delesseria sanguinea*. Svensk. Bot. Tidskr. **5**:260–324. *pls. 2, 3. figs. 16*. 1911.

come together near a nucleolus, and then become associated into tetrads. From the number of chromosomes found in tetrasporic and female plants, and the stage at which the reduction division occurs, SVEDELIUS concludes that alternation of generations occurs in the life cycle of *Delesseria* in the sense that the reviewer proposed in his investigation of *Polysiphonia*, and that is followed by LEWIS for *Griffithsia*. SVEDELIUS denies SCHMITZ and OLTMANNS' view that the gonimoblasts of Florideae represent the sporophytic phase, comparable to those of mosses, and that the tetraspores are only the special forms of reproductive cells, comparable to brood cells or "Nebenfruchtformen," and with no fixed place in the life-history.

In closing, he proposes to drop out the term "carpospores," and to substitute "carpogonidia," the reason being that the spore has the haploid number of chromosomes and represents the gametophytic phase, whereas the carpospore has the diploid number and represents only a stage in a prolonged phase of the sporophyte.—S. YAMANOUCHI.

Plant proteins.—ZALESKI[11] is making a study of the transformation of food materials in ripening seeds. The present paper deals only with the nitrogenous materials in their relation to the synthesis of proteins. By applying a method used in 1905, he finds that various non-protein organic N-containing materials are transformed to proteins during ripening. The method consisted in removing green peas from the pod and coats to avoid additions from other portions, and in making determinations of the N in proteins, in amino acids, and in organic bases. The determinations for one portion was made immediately after the removal, and for other portions 2–5 days later. In all cases considerable amounts of amino acids and organic bases were transformed to proteins. A typical analysis follows:

	Control	After 5 days storage
N of protein	79.2 per cent of total N	89.2 per cent of total N
N of amino acids	8.7	4.6
N of organic bases	10.8	5.6
N of other compounds (difference)	1.4	0.8

Under similar treatment, *Zea mais* showed little protein synthesis, and the sunflower only protein decomposition. In the pea the synthesis was less than half as fast in the absence of O_2 as in its presence. Drying of the seeds also greatly hastened the synthesis.

ZALESKI brings together the evidence for the conception that the amino acids resulting from the hydrolysis of a plant protein are the ones involved in its synthesis. He considers the two processes as two phases of a reversible

[11] ZALESKI, W., Zur Kenntnis der Stoffwechelselsprozesse in reifenden Samen. Beih. Bot. Centralbl. **27**:63–82. 1911.

reaction. This accords with the evidence on the animal side, and stands in opposition to WASSILIEFF's view that asparagin is the immediate material from which plant proteins are synthesized, and to the PFEFFER view that proteins may be synthesized by the installation of NH_3 into organic compounds without the amino acids as intermediate forms. ZALESKI raises the question whether the same enzymes cause both the condensation and hydrolysis. Both protease and rennin were found in the ripening seeds, but no tests were run for ereptase. The hydrolytic activity diminished as ripening progressed, due either to the destruction of the enzyme or to its transformation to an inactive form, for no evidence for an anti-enzyme could be found.—WILLIAM CROCKER.

Potassium in plants.—WEEVERS[12] has made a rather extensive study of the distribution of potassium in plants. He used, in the main, MACCALLUM's method of treating the tissues with sodium cobalt nitrite, followed, after thorough washing with water, by ammonium sulphide. He finds potassium in all plants except Cyanophyceae. The nucleus and chloroplast are always potassium-free, while the vacuole is rich in it, and the cytoplasm contains considerable. The writer believes, contrary to MACCALLUM, that these reagents are not capable of showing the localization of the potassium in the cell. The apparent localization found by the latter worker was probably largely due to precipitation determining the concentration gradients in both the reagent and the potassium salt. Essentially all the potassium found in the plant cell can be dissolved out of the dead cell with either water or 50 per cent alcohol, so the author believes the element exists in the form of inorganic salts and not as a part of the protoplasmic organic constituents. The pollen grains of *Tulipa* and *Crocus* are potassium-free, and will develop normal tubes in a potassium-free medium. In these cases then, among the higher plants, potassium is not necessary for growth. The absence of potassium in the chloroplasts is offered as fatal to the assumption of various workers that it plays an important rôle in photosynthesis. The author believes that his findings agree with the view that potassium in the growing point is connected with protoplasm construction, while in the vacuole it aids in the production of osmotic pressure. The facts reported in this work, agreeing in the main with those reported by MACCALLUM, show how little we know about the physiological rôle of potassium.—WILLIAM CROCKER.

Development of Laminaria.—The development of the Laminariaceae from spore to adult has been very little studied. YENDO[13] has studied the development of three forms, *Costaria Turneria*, *Undaria pinnatifida*, and *Laminaria* sp., and the results may be summarized as follows: The sporelings

[12] WEEVERS, TH., Untersuchungen über die Lokalization und Funktion des Kalium in der Pflanzen. Recueil des Travaux Bot. Néerl. **8**:289–332. *figs.* 3. 1911.

[13] YENDO, K., The development of *Costaria*, *Undaria*, and *Laminaria*. Ann. Botany **25**:691–715. *pls.* 53–55. 1911.

develop first as confervoid bodies, growing by a single apical cell. This body then becomes monostromatic, with a monosiphonous stipe. The two cells situated side by side at the same level below the apical cell initiate the monostromatic blade, and this blade becomes distromatic at base, and at the same time the monosiphonous stipe becomes polysiphonous. A new meristematic tissue appears at the transition region between blade and stipe. The growth both in length and breadth is due to the apical and stipo-frondal growth up to a certain period. The apical growth gradually diminishes and finally ceases, and then erosion of the apex of the blade follows. A single precortical layer of large parenchymatous cells is developed at the transition region between the already existing two layers. The hyphal cells are formed as the precortical layer becomes doubled, and the expansion of their distal ends into a trumpet shape takes place at the intercellular spaces. The ribs and meridional region are formed by special thickening of the cortical layers. The dorsiventrality of the lamina, if it exists, is indicated simultaneously with the formation of these parts. The cryptostomata in the Laminariaceae do not originate from a single cell.—S. YAMANOUCHI.

Geotropism.—ÁRPÁD PÁÁL[14] finds that reduction of the air pressure lengthens the geotropic reaction and presentation times in the root of *Phaseolus vulgaris*. The presentation time was 6 minutes at one atmosphere; 20 minutes at 0.74; 35 minutes at 0.21; and 70 minutes at 0.08. The reaction time was found markedly variable when all controllable conditions were constant. From the average of many measurements, the author finds that if at one atmosphere the reaction time is considered as 1, at 0.74 atmosphere it is 1.09; at 0.34 atmosphere 1.39; at 0.21 atmosphere 1.60; and at 0.08 atmosphere 2.20. It is interesting to see what slight reductions in pressure cause a lengthening of these critical times. It is well-known that the respiratory intensity is not cut until the pressure is reduced to a much greater degree. If the effects here are due to the reduced oxygen pressure, as is assumed, one sees what a complex rôle oxygen plays in the organism, the several functions apparently having very different critical pressures. The author concludes that the lengthening of the reaction time is due to the sum of the effect of reduced pressure upon the sensory and motor phases and to the telescoping of these phases.—WILLIAM CROCKER.

Formaldehyde and green plants.—GRAFE[15] finds etiolated plants or non-chlorophyll parts of green plants very sensitive to vapors of formaldehyde, especially if the cultures are illuminated. The chlorophyll-bearing parts (*Phaseolus vulgaris*) are not injured by concentrations as great as 1.3 per cent

[14] PÁÁL, ÁRPÁD, Analyse des geotropischen Reizvorgangs mittels Luftverdünnung. Jahrb. Wiss. Bot. **50**:1–20. 1911.

[15] GRAFE, VIKTOR, Untersuchungen über das Verhalten grüner Pflanzen zu Gasformigen Formaldehyde. Ber. Deutsch. Bot. Gesells. **29**:19–26. 1911.

of the atmosphere. Illuminated cultures of green seedlings in CO_2 free chambers gave much greater growth and increased dry weight if formaldehyde vapors were present than if they were not. It was necessary of course to protect the non-chlorophyll-bearing parts from contact with the vapors. Formaldehyde increases the reducing sugars in *Phaseolus* at the expense of starch deposit. This may account for the failure of starch to appear as a result of the synthesis of formaldehyde. These results, with the more telling experiments of SCHRYVER,[16] USHER and PRIESTLY,[17] and others, furnish strong evidence that formaldehyde is an intermediate product in photosynthesis.—WILLIAM CROCKER.

Phosphorus content of oat grains.—LEWONIEWSKA [18] finds that the phosphoric acid content of oat grains, measured both in absolute amount and in its ratio to the nitrogen, varies greatly with cultural conditions, involving variation in fertilizers and nature of the soil. The variation is mainly due to the inorganic and phytin phosphoric acid, and not to the protein and lecithin phosphoric acid. The author thinks that an excess in the soil leads to its storage in the inorganic and phytin forms. A variation in the nitrogen content of the grain is mainly due to the protein nitrogen. The author concludes that the phosphoric acid supply in the soil can be best judged by the ratio of inorganic and phytin phosphoric acid to protein nitrogen in the grain. The probabilities are that the conditions determining the proportion of absorption and form of storage of nitrogen and phosphorus compounds are much more complex than the author assumes.—WILLIAM CROCKER.

A new genus of yeasts.—NADSON and KONOKOTINE[19] have described a new genus (*Guilliermondia*) of Saccharomycetes, in the culture of which they observed the pairing and fusing of unequal cells ("gametes"), resulting in a cell that became an "ascus" producing one spore (sometimes two spores). In the germination of the spore under usual conditions, cells with the ordinary budding habit were produced. The full account is in Russian and the brief summary in French.—J. M. C.

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[16] SCHRYVER, S. B., Photochemical formation of formaldehyde in green plants. Proc. Roy. Soc. London B **82**: 226–232. 1910; rev. in BOT. GAZ. **51**: 470–471. 1911.

[17] USHER, F. S., and PRIESTLY, J. H., Proc. Roy. Soc. London B **84**: 101–112. 1911.

[18] LEWONIEWSKA, S., Schwankungen in dem Gehalte der Pflanzensamen an einzelnen Phosphorsäureverbindungen in ihrer Abhängigkeit von Vegetationsbedingungen. Bull. Acad. Sci. Cracovie 1911: 85–96.

[19] NADSON, G. A., and KONOKOTINE, A. G., *Guilliermondia*, un nouveau genre de la famille des Saccharomycètes à copulation hétérogamique. Bull. Jard. Imp. Bot. St. Pétersbourg **11**: 117–143. *figs. 45.* 1911.

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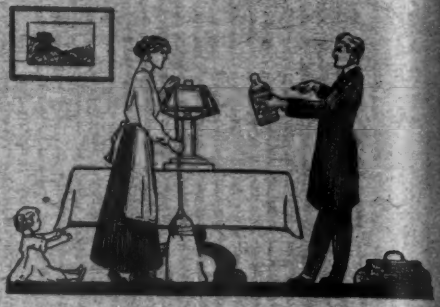

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